SPECIES RICHNESS, COMMUNITY COMPOSITION, AND SPECIES DISTRIBUTION PATTERNS IN ALEUTIAN PLANTS

By

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Abstract

We conducted an analysis of vascular plant distributional patterns in the Aleutian Islands to identify and quantify the impact of potential Aleutian Island distance dispersal barriers and ecological constraints. Data were collected from Open Access databases, printed floristic accounts, and independent collections made by the primary author to develop an Aleutian Islands floristic database. We documented 520 vascular plant species from 231 genera and 69 families across thirteen well-collected islands in the study area. The most common plant distribution pattern was 'Eastern', though it compared similarly to the 'Western' and 'Widespread' distribution pattern. We calculated and input a classic species assemblage dissimilarity measurement (Jaccard Index), a measurement of phylogenetic dissimilarity (UniFrac), and species richness into non-parametric algorithmic models (TreeNet) based on classic and Aleutians-specific island biogeography hypotheses. Aleutian plant species richness is strongly associated with the equilibrium model variables area and island isolation, as well as distance from the islands to the Alaska Peninsula, and island total stream length. Species composition, using cluster groups of the Jaccard dissimilarity metric between islands, is strongly associated with the landmass groups during the last glacial maximum, maximum island elevation, island isolation and island area. Species composition, using cluster groups of the phylogenetic-derived UniFrac distance metric, is associated with island area, distance from the islands to the Chukotka Peninsula, maximum island elevation, island geologic age, and island isolation. Altogether, this study adds to the growing body of studies extending the classical equilibrium theory of island biogeography to include additional important drivers of diversification on islands such as the landmass during the LGM, or human perturbations affecting extinction rates. Although this study included a compilation of over eighty years of collecting efforts in the Aleutian Islands, it

highlights how few “complete” floras have been assembled. The conclusions presented here highlight research targets for gaining continued insights into diversity patterns across the Aleutians.

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General Introduction

Botanical collecting efforts in Alaska have largely concentrated on easily accessible highways, river corridors, near-shore environments, and hub communities (Huettmann & Ickert-Bond, 2016). Even within well-collected areas, certain habitats such as wetlands are often left under-collected (Lipkin & Parker, 1995; Lichvar et al., 1997). We have comparatively few collections from remote areas of Alaska due to the difficulties assessing these regions. Although Alaska represents 17.5% of the U.S.A.'s land area, collection records from Alaska in the Global Biodiversity Information Facility represent only 1.2% (GBIF; http://www.gbif.org/, accessed May, 2016). This averages to approximately 3.5 specimens per square mile for Alaska, while the U.S.A. averages 52.5 specimens/square mile. The Aleutian Islands, an island chain extending in an arc west of the Alaska Peninsula runs between North America and Eastern Russia, are some of the most remote areas of Alaska. The chain is known for its fierce storms and near-constant wind, fog, and precipitation, which make field conditions difficult. In addition, accessing the islands is expensive, as there are no commercial flights other than to Unalaska and Adak.

The Aleutian chain is an island archipelago, like the Hawaiian and Galapagos islands. Many island archipelagos have been used in island biogeography studies that established relationships between environmental factors and floristic diversity measurements such as species richness and composition (Simberloff & Wilson, 1969; Juvik & Austring, 1979; van der Werff, 1983; Yeakley & Weishampel, 2000; Price, 2004). One such classic island biogeography model, the equilibrium model from MacArthur and Wilson's *Theory of Island Biogeography* (1967), proposes that the number of species found on an island can be determined by a balance between the immigration rate (or the movement of species onto the island from other islands) and the extinction rate (or the rate at which species already on the island become nonexistent).

Immigration and extinction rates are affected by island size, isolation and age, to predict species richness. The expectation is that species richness increases with increasing area, decreases with further distance from the mainland source, and that every island can be fit to this model.

Following the publication of these classic models, numerous studies have highlighted that there are numerous other geological and environmental factors that affect both species richness and distribution (Stuessy et al., 1998). While the equilibrium model is still widely regarded, it has been suggested that a "new paradigm" is emerging in regard to island biogeography (Lomolino, 2000; Heaney, 2007). This 'new paradigm' involves new improvements and analyses addressing the criticisms of the equilibrium model. It also allows researchers to describe new processes governing species assemblages. For example, the increasing availability of phylogenetic information has allowed researchers to combine genetic data with distributional data to test biogeographical hypotheses in a statistical framework (Sanmartín et al., 2008). Genetic divergence may be leveraged in a Bayesian approach to island biogeography to help answer questions of dispersal versus vicariance in speciation and distribution (Sanmartín et al., 2010), or may provide insight into the historical constraints of the distributions of species between islands (Kubota et al., 2011). A better understanding of historical constraints on species distribution has also helped corroborate the hypothesis that species may evolve on islands and recolonize the mainland (Dávalos, 2007; Heaney, 2007; Bellemain & Ricklefs, 2008). These analyses have allowed for new conclusions about even well-studied island systems such as Krakatoa (Bush & Whittaker, 1993) and the Ryukyu Islands (Kubota et al., 2011), and have demonstrated that these approaches to island biogeography will have powerful ramifications to our understanding of island systems in the future.

For the Aleutian Islands, using the equilibrium model as a baseline for our investigation, it is important to identify and quantify additional factors that may move floristic measures such as species richness and composition "out of equilibrium". Given its history of glaciation, one such possible influence is how the Aleutian Islands were split into several large landmasses during periods of lower sea level during the last glacial maximum. Studies have suggested that the species area relationship is influenced not only by current island area, but there is also predicted increasing species richness with historically larger areas such as during the last glacial maximum (Lindroth, 1961; Weigelt et al., 2016). As an additional potential factor, the Aleutians have a tremendous amount of historical and recent geologic activity (Hultén, 1937; Heusser, 1990; Talbot et al., 2010b). As a part of the Pacific Ring of Fire, there are approx. 52 volcanoes across the island chain, with 30 of them historically active in the last 20 years. Multiple eruptions have occurred, including on Kasatochi where the vegetation and animal life was almost completely extirpated (Talbot et al., 2010b).

Despite the remoteness of the Aleutians, there are also observable direct and indirect human impacts across the Aleutian chain. Following the large removal of sea otter populations by Russian fur traders in the 1800s, foxes were introduced on many islands to supplement the fur industry. Rats were also incidentally introduced to the islands. Rats and foxes cause a trophic cascade on islands where they have reduced the organic seabird and waterfowl populations (Croll et al., 2005; Maron et al., 2006). Caribou, reindeer, and cattle have also been introduced to several Aleutian Islands (Ricca et al., 2012). There has also been a long history of human inhabitation of the Aleutians dating back to the first settlement by the Aleuts. It is estimated that there were 15,000-25,000 Aleuts in the chain at first contact with Russians in the 1800s (Lantis, 1984). Russians created fox farms and settlements across the chain, and the islands were further

impacted by the WWII Japanese invasion, which led to a bombing campaign and developments of airstrips, forts, and bases across the chain, the legacy of which still persists (Byrd & Springer, 1976). Largely as a result of WWII and Cold War activities, contaminated sites are present on nearly every mid-sized and greater island in the Aleutian chain, as identified by the Alaska Department of Environmental Conservation's Contaminated Sites Program Database (http://dec.alaska.gov/spar/csp/db_search.htm, accessed October 18, 2016). On Adak Island alone, 181 areas of chemical and/or petroleum contamination were evaluated, and over 200 areas of potential unexploded ordnance were identified (https://dec.alaska.gov/spar/csp/sites/adak.htm, accessed October 18, 2016). Contaminated sites present carcinogenic and non-carcinogenic hazards to human health and the environment, and may bio-accumulate into top predators such as bald eagles (Stout & Trust, 2002).

Due to its inaccessibility and harsh environment, few detailed botanical studies have been completed on the Aleutian Islands. The first compilation of an Aleutian flora was likely *A contribution to the flora of the Aleutian Islands* by Tatewaki & Kobayashi (1934), who visited the islands of Attu, Amchitka, Atka, Umnak, and Unalaska between 1929 and 1931. They performed a thorough botanical investigation and published a list of 244 species and identified several dozen community-types on the islands. Swedish botanist Eric Hultén visited 13 islands and collected over 2,500 specimens for his *Flora of the Aleutian Islands and westernmost Alaska Peninsula: with notes on the flora of Commander Islands* (1960). Since Hultén's work there have been several detailed single-island surveys in the Aleutians: Amchitka Island (Shacklette et al., 1969; Amundsen & Clebsch, 1971); Buldir Island (Byrd, 1984); Attu Island (Talbot & Talbot, 1994); and Unalaska Island (Talbot et al., 2010a). However, few studies have examined diversity patterns across the Aleutian Islands to understand the drivers of floristic assemblage. McCord

(1980) examined the phytogeography across the Aleutian and Bering Sea Islands and concluded that the vascular plant species number was correlated with island area. Unfortunately, many under-collected islands were included in the analysis by McCord (1980), which may have skewed the species/area relationship analysis, as well as confounding the relatedness between islands. More recently, a study of 18 islands in the Aleutian chain concluded that increased species diversity and richness on small islands were associated with the presence of introduced rats and foxes, which thwart the marine-derived nutrient subsidies provided by seabird colonies (Croll et al., 2005; Maron et al., 2006). However, this study was confined to islands that are less than 20 km^2 in area. Although all of these studies have contributed to the advance of botanical knowledge of the Aleutian Islands, there are still large gaps in knowledge of the Aleutian flora and we are far from an understanding of what has shaped the currently observed floristic diversity.

Another interesting aspect of the Aleutian Islands is their proximity to the Northern Bering Sea Islands. Hultén (1937) identified an area containing the Northern Bering Sea and the Aleutian Islands as the "center of an equiformal, progressive group of plant species", and several other studies have suggested a floristic similarity between the two island groups because of their oceanic influences and relative proximity (Hultén, 1937; Hultén, 1961; Yurtsev, 1972; Yurtsev, 1994; Elvebakk et al., 1999; Elven et al., 2011). Climatically, the Aleutian Islands and the Northern Bering Sea Islands share persistent high winds and precipitation, and are similarly treeless (Young, 1971; Talbot et al., 2010a). Due to this perceived similarity, a detailed study of the Aleutians would greatly improve any future comparison.

In this study, we aim to increase the botanical knowledge on poorly collected or incompletely collected Aleutian Islands by visiting under-collected islands to directly investigate

the flora. Through our informed collecting efforts, consolidation of records in a unified taxonomy, review of museum records, and with techniques utilizing both the fossil record and phylogenetic data, we aim to determine significant historical and current geographical factors associated with species diversity and richness in the Aleutian Islands. The addition of the fossil record and phylogenetic data to our current species distribution data will allow us to analyze the current phylogenetic relatedness between islands, to reveal the effects of historical constraints on current plant species assemblages (Graham & Fine, 2008).

Chapter 1:

Species richness, community composition, and species distribution patterns in Aleutian plants[1]

Introduction

Islands are natural scientific laboratories. They represent interesting study systems, as different patterns of species richness, endemism, and species turnover may be examined in an isolated environment (Wallace, 1902; MacArthur & Wilson, 1967; Simberloff & Wilson, 1969; Losos & Ricklefs, 2009). Of particular importance for the study of biota assembly on islands has been the *Equilibrium Model of Island Biogeography* which proposes that immigration, speciation and extinction should vary predictably, as determined by three factors: the time since system initiation (i.e., island formation), the isolation of the environment, and the area of the environment (MacArthur & Wilson, 1967). The balance of arrival of new species through colonization and the disappearance of old species due to extinction, expressed as the equilibrium model, is one of the most influential theories within ecological biogeography (Whittaker et al., 2008) and is now being used in conservation biology (see sources and sinks, e.g. Pulliam, 1988; Runge et al., 2006). The equilibrium model has been applied to many island archipelagos to help understand species richness, species turnover, and extinction, including the Hawaiian (Juvik & Austring, 1979; Price, 2004) Galapagos (van der Werff, 1983; Yeakley & Weishampel, 2000), and western Pacific islands (Adler & Dudley, 1994; Whittaker et al., 2008). The species-area relationship, in particular, has been a focus of many studies (Schoener, 1976; Connor & McCoy,

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1979; Angermeier & Schlosser, 1989; Lomolino, 2000a; Lomolino & Weiser, 2001).

Size and isolation alone are often insufficient to explain species richness on islands, however, as numerous geological, ecological, and historical factors may determine the total number of species supported (Stuessy et al., 1998; Kreft & Jetz, 2007; Weigelt et al., 2016). For example, the increase in availability of phylogenetic information has allowed researchers to combine genetic data with current distributional data to measure species assemblage dissimilarity using phylogenetic distance (Sanmartín et al., 2008). Environmental survival and dispersal ability are, in part, phylogenetically determined (Pearman et al., 2008), therefore, the dissimilarities of phylogenetic structure within insular assemblages may indicate the constraining effects of geohistorical processes (Graham & Fine, 2008). In an application of this concept, phylogenetic dissimilarity has been utilized to provide insight into the historical constraints of the distributions of species between islands in the Japanese Ryukyu Islands (Kubota et al., 2011).

Identifying and quantifying the dispersal barriers (also referred to as "geohistorical" barriers; Kubota et al., 2011) and/or ecological constraints (i.e., "habitat filtering"; Cornwell et al., 2006), which have acted on plant dispersal and development are important factors for understanding area plant assemblages (Kubota et al., 2011). They are particularly important in island chains, which often lie between sources of highly dissimilar plant assemblages. The presumably small influence of a single ecological constraint or dispersal barrier may limit the distribution of a regional flora. This has been observed in the Galapagos Islands, where the presence of steep elevational gradients on the islands nearest to the South American mainland has acted as a dispersal barrier (Yeakley & Weishampel, 2000). It could be predicted that many island groups would act as "stepping stones" for plant dispersal and would homogenize across their entirety. However, dispersal barriers and ecological constraints reduce the capability of

plant species to travel between an island source and a nearby target (Thornton et al., 2002; Silvertown, 2004; Kadmon & Allouche, 2007).

In Alaska, we have outstanding opportunities to study island systems. For instance the Bering Sea Islands, Alexander Archipelago, Kodiak Archipelago, Prince William Sound Islands, and Aleutian Islands are all large island groups and present isolated study environments. The Aleutian Islands are a long chain of mostly volcanic islands which run west of the Alaska Peninsula toward the Russian Kamchatka Peninsula, arcing between 51° and 56° N latitude (Fig. 1). There are over 300 islands in the Aleutian arc. Permafrost is absent from the Aleutians and relatively high average temperatures are common (Tatewaki & Kobayashi, 1934; Yurtsev, 1994; Elvebakk et al., 1999). Numerous active volcanoes in the chain contribute to a rugged topography. The highest point in the chain is the volcanic Mount Shishaldin (2857 m) on Unimak Island (Fig. 1). The Aleutian Islands are treeless, and although the coastline is lush, the vegetation on the island arc is often characterized as "maritime tundra" (Hultén, 1960; Maron et al., 2006). This island chain is an ideal island study system because of the islands' similar latitudes and soil types (Maron et al., 2006).

There are multiple quantifiable environmental factors on the Aleutian chain that may influence patterns of plant assemblage. For example, as proposed in the Equilibrium Model, the time since system initiation (i.e., island formation), the isolation of the environment (i.e., distance from the nearest island), and the area of the environment are three important factors influencing immigration, speciation and extinction in an island environment (MacArthur & Wilson, 1967). Maximum elevation can serve as an indirect measurement of island topography and may be associated with a larger number of ecological niches (Ricklefs & Lovette, 1999). In addition, the presence of active volcanoes may be utilized as an indirect measurement of the

probability that an island has experienced recent ecological disturbance. Volcanic eruptions may destroy or greatly disrupt an island's vegetation, as seen on Kasatochi Island in the Aleutians (Talbot et al., 2010b), the Icelandic volcanic island Surtsey (Magnússon et al., 2009), and the Krakatau Islands (Whittaker et al., 2000). It has also been proposed that island biogeography is in many instances now dominated by the activities of human populations as we now live in the "Anthropocene" epoch, where ecosystems are dominated by global human influence (Helmus et al., 2014).

In a broad sense, plant distributions are globally distributed by climatic gradients, though local distributions may be determined through competition, species climatic sensitivity, and other local factors (Woodward & Williams, 1987). As an island chain of relatively similar climate, latitude, and soil types (Maron et al., 2006), it is widely accepted that plant distributional patterns in the Aleutian Islands reflect palaeogeographical influences such as direct and indirect effects of glaciation, including the effects of sea level changes on distances between islands (Hultén, 1937; Tatewaki & Kobayashi, 1934; Lindroth, 1961; Heusser, 1990). Alternatively, several recent studies (Croll et al., 2005; Maron et al., 2006) suggest that seabirds have created a "habitat filter" across the island chain. This 'filter' is created when seabirds provide both abundant nutrient subsidies and direct physical disturbance of the vegetation. This influence separately or additively selects for specific plant compositions and abundances across large island areas. The human disturbance of seabird habitats with the introduction of invasive predatory mammals, is an example of one of the many potentially important human-related influences on the Aleutian Islands plant assemblages.

To examine these potential climactic, geographical, and anthropogenic influences in the Aleutian Islands we conducted an analysis of plant distributional patterns. Integral to this

examination was how floristic patterns would be represented. Although species richness is a feature of the equilibrium model, there are numerous dissimilarity coefficients that vary based on their suitability for different applications and input data, and represent appropriate measures of Aleutian Island floristic composition (Faith et al., 1987). The Jaccard dissimilarity index, which was developed to compare regional floras (Jaccard, 1912), is a classic dissimilarity measurement that is useful for detecting underlying ecological gradients between communities (Faith et al., 1987). Phylogenetic (DNA-based) dissimilarity measures, such as UniFrac, may also be used as an alternative measurement of island dissimilarity. As environmental survival and dispersal ability are phylogenetically determined (Pearman et al., 2008), phylogenetic dissimilarity may reveal the historical constraints of environmental differences across a system, if there is a strong ecological gradient (Kubota et al., 2011).

Several methods may be utilized to identify and quantify the impact of an island group's distance dispersal barriers and ecological constraints, once appropriate dissimilarity measurements and environmental variables have been identified and quantified. Phylogenetic dissimilarity between islands, for example, has been analyzed using the Multiple Regression on a distance Matrix approach (MRM; Nakamura et al., 2009). However, the use of linear regression models (such as MRM) in ecology is not ideal because of the required high level of statistical knowledge required to describe large ecological data sets (Oppel et al., 2009). Furthermore, ecological relationships are virtually never linear or parametric (e.g., De'ath & Fabricius, 2000, Whittingham et al., 2006).

Non-parametric algorithmic models, such as those generated in TreeNet analyses (i.e. boosted regression trees; Salford Systems, 2001) are more robust. They are known to cope better with large numbers of predictor variables with limited observations (Craig & Huettmann, 2008,

Hegel et al., 2010). In data mining TreeNet analyses, predictor variables can be either categorical or continuous and the algorithm makes 'best' use of predictors offered, allowing for a large number of predictor variables to be included (Cutler et al., 2007; Oppel et al., 2009). Analyses combining phylogenetic dissimilarity between islands and a TreeNet analysis provide an ideal and rational examination of the historical constraints influencing floristic assemblage in an island system when the use of latest methods and data mining is the goal. If these methods are applied using Open Access data then they also become transparent and can be repeated, allowing for powerful inference that is difficult to reject.

In the current study, we aim to identify, quantify, and visualize the most important variables that influence the pattern of plant species assemblages in the Aleutian Islands using best available data and methods. In these analyses we have input cluster groups derived from a classic species assemblage dissimilarity measurement (Jaccard Index), cluster groups derived from a measurement of phylogenetic dissimilarity (UniFrac Metric), and species richness as response variables.

Materials and Methods

Acquiring Regional Species Data – The floristic composition of the Aleutian Islands used here was primarily based on herbarium specimens from the University of Alaska Museum database ARCTOS (http://arctos.database.museum, accessed October 10, 2012). Searches in ARCTOS were made using the "Locality" search option with island names specified. Plant taxon names and locality information were downloaded from ARCTOS and then converted into a spreadsheet. Published and unpublished island floras (Hultén, 1960; Shacklette et al., 1969; Amundsen, 1977; McCord, 1980; Byrd, 1984; Talbot & Talbot, 1994; Golodoff, 2001; Kenney & Kaler, 2010;

Talbot et al., 2010a; Jones, 2011; Freeman & Garroutte, 2012) based on museum voucher specimens were also used as supplementary sources for assembling regional taxon lists and were manually entered into spreadsheets (see attached file Supplemental A). Furthermore, vouchered and identified collections from the author's visits to several Aleutian Islands were added to the taxon lists (Adak Island: July 30-31, 2010, July 27-31, 2011; Buldir Island: August 3-26, 2010, August 5-27, 2011; Rat Island: August 28, 2010; Attu Island: August 2-3, 2011; Kiska Island: August 29, 2011; Fig. 1 & 2). Species nomenclature follows the Pan Arctic Flora (Elven et al., 2011; http://nhm2.uio.no/paf, accessed March 1, 2016) and the Flora of North America (Flora of North America Editorial Committee, 1993). For taxonomy at the family level and above, the Angiosperm Phylogeny Group III project (APGIII; Bremer et al., 2009) was consulted. Synonymous species names were merged into a single entry.

Species Characteristics – Each species included in the regional taxon data table was assigned values for several categories, including ploidy, growth form, and species lifespan (see attached file Supplemental A). Ploidy level was scored as either diploid or polyploid, determined by the number of sets of chromosomes present in a cell. Polyploidy has been linked to greater ability to survive in small populations (such as on isolated islands; Lumaret et al., 1997), and has been associated with species invasiveness (te Beest et al., 2012). Species that were cited to be both diploid and polyploid were recorded as both, based on references in the Pan Arctic Flora (Elven et al., 2011), the Flora of North America (Flora of North America Editorial Committee, 1993), or the Index to Plant Chromosome Numbers (Goldblatt & Johnson, 1979; http://www.tropicos.org/Project/IPCN, accessed March 1, 2016;). Growth form for each species was determined to be graminoid, shrub/subshrub, forb, or fern/fern ally, as determined from

observation or general knowledge of the family or genus. Taxon lifespan was coded as either perennial or annual, as indicated, preferentially, in the Pan Arctic Flora (Elven et al., 2011), the Flora of North America (Flora of North America Editorial Committee, 1993), or the USDA PLANTS Database (USDA & NRCS, 2016; http://plants.usda.gov, accessed March, 2016). Species observed to be both perennial and annual were recorded as 'both'.

Species Distribution Data – Species distribution data were collected to examine species distributional patterns and their frequency. Following the compilation of a regional taxon data table for the Aleutian Islands, and the assignment of each species to islands in the study area based on their presence or absence, each species was assigned a classification based on its distribution pattern across the study area. Distribution pattern classifications were based on the presence or absence of a species within the four main islands groups that stretch east-west (Fig. 1). The occurrence frequency of genera, families, and species characteristics on each island in the study area were also determined once species distribution data were collected.

In addition, the regional taxon data table was compared to plant species lists from multiple regions in Eastern Russia and Alaska, compiled by Ickert-Bond et al. (2013) from the University of Alaska Museum database ARCTOS and from the *Checklist of the Flora of the Chukotkan Tundra* (Yurtsev et al., 2010) as well as the *Checklist of Wrangell Island* (Petrovsky, 1988). Additional floristic information was obtained from the *Flora of the Commander Islands* (Mochalova & Yakubov, 2004), and the *Flora of Kamchatka* (Yakubov & Chernyagina, 2004). This comparison was utilized to determine which species in the study area were also present or lacking in each of these regions for inclusion in the matrix. As a third distributional indicator, species occurrence data from the Global Biodiversity Information Facility (GBIF;

http://www.gbif.org/, accessed March 15-16 and April 3-4, 2016) was downloaded for the identified geographic regions in Russia and Alaska. Searches in GBIF were made using the "Occurrence" search, with "Plantae" specified as the "Scientific Name" parameter, and geographical coordinates entered into the "Location" parameter to specify a bounding box or polygon of the search area (see References for GBIF search data download links).

The regional taxon data table was compared to these occurrence lists. Co-occurring species in both the study area and each region were recorded. Species assemblages from individual islands in the study area were also directly compared to the nearest adjacent regions, including the Kamchatka Peninsula, the Alaska Peninsula, and the two region composites comprised of all the adjacent regions in Russia and Alaska, referred to as "Alaska Mainland" and "Eastern Russia". Both the number of species and the proportion of the islands' species shared with the adjacent regions were calculated and added in the analysis (see attached file Supplemental A).

Islands Included in the Analysis – Species counts must be accurate, or at least be representative, for testing various area-number relationships in island groups. Therefore, only those islands that we deemed "well-collected" were included in the final analysis. To be deemed well-collected, islands had to include more than 150 vouchered collections from searches in ARCTOS, other online databases, published and unpublished floras, or independent collections by the author. A cut-off point of 150 was chosen as a general number of collections, which implied a minimal threshold of effort was expended for documenting the flora on that island (i.e. approximately 80%). The Aleutian Islands meeting the "well-collected" criterion were Adak, Agattu, Alaid, Amchitka, Akutan, Atka, Attu, Buldir, Kiska, Rat, Umnak, Unalaska, and Unimak (Fig. 1).

Island Characteristics – Multiple geological characteristics and geographical distances were identified and quantified for each of the islands in the study area. The maximum elevation (m) of islands was determined using USGS topoView (http://ngmdb.usgs.gov/maps/topoview/, accessed April, 2016), while volcanic islands were identified using the USGS/Alaska Volcano Observatory database (http://www.avo.alaska.edu/volcanoes/, accessed August 10, 2013), which indicated the presence of volcanoes, and which volcanoes were considered historically active, active in the Holocene, or active within at least the last two million years. Island areas (km^2), mapped stream length (km), number of bays, and geologic ages (determined by how many ages of rock were present on the island) were taken from McCord (1980) and tabulated (Table 1). Islands with a history of fox introduction (i.e., islands with extirpated seabird colonies) and islands with native red fox populations (the far-eastern Aleutian Islands) were recorded for the analysis, although this was not expected to be an important predictor since it was determined that only one island in the study (Buldir) had no historical fox introduction or native fox population (Table (1) & Fig. 3). Islands with either native or introduced caribou, introduced reindeer, or introduced cattle populations were also recorded for analysis (Table 1 & Fig. 3).

Other Potentially Influential Predictors Included in the Analysis – The geographic distances (km) between islands, island latitude (°N), distance from the Alaska Peninsula, the Kamchatka Peninsula, the Southeast Alaska Coast, the Alaska Yukon Plain, the Seward Peninsula, the Chukotka Peninsula, and distances from known geologic gaps (e.g., Buldir Gap, Amukta Pass, Amchitka Pass; Fig. 1) were measured manually using Google Earth (km; https://www.google.com/earth/, accessed August, 2013). For distances from geologic gaps that are situated inside the Aleutian chain, islands to the west of the gaps were given negative

distance values, while islands to the east of the gaps were given positive values. These measurements provided a quantitative measure of distance for each island from each geographical gap, differentiated into two groups based on which side of the gap they were found. Distances from Amukta Pass (70 km), Amchitka Pass (96 km), and the Buldir Gap (230 km) were included in the analyses (Fig. 1). Bathymetry was used as an approximation of which islands in the study area would have been part of larger landmasses during the last glacial maximum when sea levels were estimated 120-135 m lower than at present (Clark & Mix, 2002; U.S. Department of Commerce, National Oceanic and Atmospheric Association, National Ocean Service Coast Survey Charts #16011 and #16012; http://www.charts.noaa.gov/OnLineViewer/AlaskaViewerTable.shtml, accessed March 15, 2016; Fig. 1).

Calculating Dissimilarity Using Species Presence/Absence – The Jaccard dissimilarity index was calculated between the Aleutian Islands (Jaccard, 1912), as a measure of species assemblage dissimilarity using the function Vegdist in the package 'vegan' (Oksanen et al., 2016) in R 3.0.2 (R Development Core Team, 2011).

Calculating Dissimilarity Using Phylogenetic Diversity – To determine the phylogenetic dissimilarity between Aleutian Islands, an Aleutian phylogenetic tree composed of all the species in the study area was constructed from an APGIII-derived "megatree" using the software package Phylomatic 3.0 (Webb & Donoghue, 2005; Bremer et al., 2009), referencing the methods used in Kubota et al. (2011). Tree branch lengths in the resulting Aleutian phylogenetic megatree were then adjusted using the bladj in Phylocom 4.2 (Webb et al., 2008) to reflect the

phylogenetic distance between plant families using fossil-based inferences of angiosperm family ages (Wikström et al., 2001). The phylogenetic beta diversity between islands was then calculated using the unweighted UniFrac distance metric (Lozupone & Knight, 2005) using the function UniFrac in the R package 'phyloseq' (McMurdie & Holmes, 2013).

Clustering Response Variables – Aleutian Island dissimilarity matrices were transformed to cluster values for input into the TreeNet models. The Jaccard dissimilarity matrix was clustered with the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) using the function Agnes in the R package 'cluster' (Maechler et al., 2012), to reveal how the islands would be clustered based on their Jaccard dissimilarity (Michener & Sokal, 1957). The phylogenetic UniFrac distance matrix, derived from the Aleutian phylogenetic megatree, was also clustered with UGPMA, to group the islands based on their phylogenetic dissimilarity. Each cluster dendrogram was visually grouped into subclusters (Fig. 4).

Compiling Response Variables – Multiple response variables were compiled from the dataset to provide alternative sets of response indices between Aleutian Islands for input into the models. This included both the cluster groups of the Jaccard dissimilarity and UniFrac distance, but also included tables of island family, genus, and species richness, as well as the frequency of perennials, annuals, forbs, shrubs/subshrubs, graminoids, ferns/fern allies, diploids, and polyploids, and their proportions by the total island species number (Table 2). Proportions and frequency of specific genera and families by island were also explored as a potential response variable.

Correlations Between Variables – Correlations between the sets of both response and predictor variables were calculated using the function varclus - Variable Clustering, in the R package 'Hmisc' (Harrell, 2008). Using varclus, correlations between variables were identified and were used to "prune" datasets for input into different models, to identify potential multicollinearity, and to guide the interpretation of analyses. Correlations were calculated using a non-parametric Spearman's rank-order correlation (Croux & Dehon, 2010), and the results were clustered using hierarchical clustering (Fig. 5).

Modeling – Non-parametric algorithmic models were favored for modeling the association between several response variables that describe the regional taxon dataset and the predictors, as parametric and/or linear ecological relationships are virtually nonexistent (De'ath & Fabricius, 2000, Whittingham et al., 2006). Machine learning methods such as classification trees (Breiman, 2001) were utilized, as they may analyze categorical or continuous variables, account for complex ecological interactions between variables (Guisan et al., 2006), and are not confounded by outliers or multi-collinearity between variables (Vayssiéres et al., 2000). Analyses were carried out using the TreeNet software, a module of Salford Predictive Modeler 8.0 (Salford Systems, 2001). The TreeNet software was utilized to construct multiple boosted regression trees to investigate the possible significance of the predictor variables on patters of species richness and species similarity. Given that there were few observations in the dataset (13 islands) and multiple predictors (20), in a traditional analysis the dataset for the current study can be considered to lack sufficient degrees of freedom. However, new analytical methods allow researchers to overcome this problem. To overcome the dataset size limitations, with an initial set of 13 island rows, and 20 predictor columns, the dataset had to be cloned (Lele et al., 2007).

The dataset was cloned four times; models using the same variables and parameters were run for each clone set. Both the species richness ('Total_sp') and the island cluster group number derived from non-phylogenetic species dissimilarity distances ('Jaccard') response variables were used for testing cloning sensitivity. Iterative models were run to assess stability with increasing dataset clones. Cloning the original dataset resulted in increased R^2 values with additional clones, and a decrease in the mean squared error (MSE) between clones. Model results from each clone were compared, and it was determined that additional clones had not modified the important variables for either response variable. Cloning had not greatly skewed the model results and the four cloned datasets could therefore be used for additional modeling in a robust fashion.

Potential response variables were correlated and then clustered into three subclusters (Fig. 5A). At least one variable from each major subcluster was included in subsequent analyses as the response variable to determine if the different sets of predictors were associated with different uncorrelated facets of the floristic composition across the islands. The "Total Species" variable (i.e. species richness) and Jaccard dissimilarity cluster groups were the primary response variables modeled for approximating species richness and similarity between islands.

Several models were developed from the dataset for each response variable. All response variables were input into a model with all twenty available predictors (the 'All (20)' model) and one with all non-categorical predictors (the "non-categorical (15)' model). The second model run with all three response variables was the 'Ecological Niche (6)' model, which included the predictors of maximum elevation (Elev), number of bays (Nbay), total stream length (Str_km), the island's history of volcanic activity (Volc), the approximate island latitude (Lat), and island area (Area). A third model, which attempted to focus on island disruptions (the 'Distruption (4)'

model), was run using the island geologic age (GeoA), island volcanic activity (approximating potential eruption effects; Volc), whether foxes had been introduced or were native to the island (Fox_int), or if large mammals had been introduced or were native to the island (LargeMamm). The equilibrium model ('Equilibrium (3)'), which describes the influence of island area, isolation, and island age, was approximated with the island area (Area), distance to nearest island (D_NI), and geologic age (GeoA) predictors. Interpretation was assessed based on model scores and variable importance. Regression models were run with the species richness response variable (Total_Sp), and models were assessed by the area under the receiver operating characteristic curve (ROC), mean squared error (MSE), and R^2 values. Classification models were run with the island cluster group number derived from non-phylogenetic species dissimilarity distances (Jaccard) and the phylogenetic cluster groups' (UniFrac) response variables, and were assessed with classification accuracy, ROC, average negative log-likelihood (Avg. LL (neg.)), and tree misclassification rate. Partial dependence plots were generated for the most important predictor variables in the best model for each response variable. These plots exhibit the relationship between the response and a predictor with compensation for the influence of the other variables in the model.

Results

Species Richness – A total of 520 vascular plant species in 231 genera and 69 families are present on the 13 well-collected Aleutian Islands. Out of the total, 11 plant species are present on all 13 islands. The species richness on each well-collected island ranged from 74 (Alaid) to 366 (Unalaska) species (Fig. 6). Species richness by area ranged from .06 species/km^2 (Unimak) to 10.7 species/km^2 (Alaid), with an average of 1.87 species/km^2/taxon (Table 2).

Species Characteristics – The breakdown on species' characteristic proportions by island is visualized in Fig. 6. The polyploidy/diploid ratio showed a high percentage of polyploid species and varied across islands in the study area from a ~55% polyploidy/diploid ratio on Unalaska Island to a ~66% polyploidy/diploid ratio on Rat Island. The average polyploidy/diploid ratio by island was ~60%. Due to taxonomic uncertainty or a lack of data, I was unable to determine the ploidy level for 31 species. Species growth form data indicated that the species in the study were separated into the following numbers and total proportions: Forbs (295 species, ~56.7% of total), graminoids (127, ~24.4%), shrubs/sub-shrubs (58, ~ 11.1%), and ferns/fern allies (41, ~7.9%). 494 species are perennials (~ 95% of the total species), and 35 are annuals (see attached Supplemental A).

The most speciose genera and families in the dataset are visualized in Fig. 7. For both genera and families, those with one taxon in the dataset were most frequent, including 24 families and 139 genera. Poaceae (64 species), Asteraceae (40 species), Cyperaceae (32 species), and Brassicaceae and Rosaceae (both with 27 species) are the families with the largest number of species in the dataset (Fig. 7A). *Carex* (26 species), *Ranunculus* (15 species), and *Poa* (13 species) are the genera with the most number of species in the dataset (Fig. 7B).

Species Distributions – Five distributional patterns were recognized that categorized the species as generally fitting into a Western, Central, Endemic, Eastern, Disjunct, or Widespread class (Fig. 8). The most common pattern was the Eastern pattern, with 141 species (27.1%), followed by the Western pattern, with 131 species (25.2%). The third most common pattern was Widespread, with 116 species (22.3%), followed by 95 species (18.3%) that showed a Disjunct

pattern, and 37 taxa (7.1%) were restricted to the Central island groups (The Rat and Andreanof Islands; Fig. 8).

The number of shared species between the study area and adjacent regions ranged from 255 shared with the Alaska Peninsula, to 27 shared with Inland Eastern Russia (Fig. 9). In a comparison of the study area with the composite of adjacent regions of Eastern Russia and Mainland Alaska, 295 species were shared with Eastern Russia, and 363 with Mainland Alaska.

In direct island-to-adjacent region comparisons, island species assemblages shared from 39 (Alaid) to 195 (Unalaska) species with the Alaska Peninsula. Islands shared 31 (Rat) to 147 (Unalaska) species with the Kamchatka Peninsula, 49 (Alaid) to 266 (Unalaska) species with the Alaska Mainland and 41 (Alaid) to 214 (Unalaska) species with Eastern Russia. In the direct island-to-adjacent region comparisons, Unalaska Island shared the most species with all of the regions compared. Overall, our data did not support a clear pattern of an increasing total number of species shared with west-adjacent or east-adjacent regions with geographical proximity. When shared proportions of the island assemblages were plotted, however, there was a supported linear trend (R^2=0.6911) of increasing shared proportion from west to east towards the Alaska mainland. There was no support for a linear trend of increasing shared proportion with either the Kamchatka Peninsula or Eastern Russia, in either direction (see attached Supplemental A).

Characteristic of Islands – Island area ranged from Alaid's 6.9 km^2 to Unimak's 4069.9 km^2, with an average of 970.4 km^2 and a standard deviation of 1279.8 (Fig. 10). Maximum island elevation ranged from Alaid's 29.6 m to Unimak's 2856.9 m, with an average of 1116.9 m and a standard deviation of 851.57. Seven islands were categorized as "volcanic", including Adak, Akutan, Atka, Buldir, Kiska, Umnak, Unalaska, and Unimak. Kiska, Atka, Umnak, Unalaska,

Akutan, Unimak have volcanoes that are considered "historically" active, while Buldir and Adak have volcanoes that were active in the Holocene. The number of bays ranged from 0 on Buldir and Alaid to a reported 50 bays on Unalaska. Mapped stream length ranged from 4 km on Alaid, to 1845 km on Umnak. Island latitudes ranged from 51.3 to 54.8 degrees north. Distance to the nearest island ranged from Unimak's 0.6 km to Buldir's 98 km, with an average of ~15.8 km. Distances from the Kamchatka Peninsula ranged from Attu's 702 km to Unimak's 2101 km, and distances to the closest point on the Alaska mainland, ranged from Unimak's 3 km to Attu's 1538 km. Islands were grouped into three categories based on geologic age, with Buldir, Alaid, and Akutan representing the youngest islands, while Umnak and Adak were the oldest group of islands. The investigation of connected landmasses during periods of lowered sea level during the last glacial maximum indicated that the well-collected islands in the study would be grouped into four larger landmasses, with all islands east of Umnak joined to the North American continental landmass (Table 1 & Fig. 1).

Island Clustering Based on Dissimilarity – Using unweighted pair group mean-averaging, the Aleutian Islands were clustered into two different statistical trees, one based on the Jaccard dissimilarity matrix of species presence/absence (Fig. 4A), and one calculated from the phylogenetic unweighted UniFrac distance matrix (Fig. 4B). The Jaccard and UniFrac tree topologies are similar in showing four distinct clusters of islands (Fig. 4). The membership of islands in the respective clusters differs between the two different measures of dissimilarity.

Clustering Correlated Model Input Variables – As outputs of the varclus function, response variables and predictors were clustered into two different dendrograms based on their correlation

strength (Fig. 5). The cluster of response variables split broadly into three correlated clusters (Fig. 5A). The cluster of predictors (Fig. 5B) shows five distinct clusters of correlated variables.

Modeling – Using the island characteristics and species distributions by island data, modeling 500 regression trees, indicated that for the species richness response variable (Total_sp, regression), the best of the five models was the all non-categorical predictors model ('Non-categorical (15)'; Table 3). This model indicated that the species richness variable is most associated with island area (Area), distance to the Alaska Peninsula (D_AKP), island isolation (D_NI, distance to nearest island), and the total length of streams on the island (STR_KM; Fig. 11). Overall, 9 of the 20 predictors were identified as important in this model, which had a ROC of 0.92594 (R^2=0.62147).

The partial dependence plot using the Area predictor indicated that, given the influence of the other predictors in the model, there is a plateau in species richness for islands between ~300-1800 km^2 (Fig. 12). A second plateau in species richness was identified at 2700 km^2 and greater. The partial dependence plot of the second most important predictor, distance to the Alaska Peninsula (D_AKP), indicates that there is a decrease in species richness in islands which are separated from the Alaska Peninsula by ~250 km or more.

Using the same dataset, modeling 500 classification trees, the best model for the island cluster group number derived from non-phylogenetic species dissimilarity distances (Jaccard, classification) was the all-available predictors model ('All (20)'; Table 3). This model indicated that the non-phylogenetic cluster groups (Jaccard) response variable is most associated with the landmass groups during the last glacial maximum (LGM_SL), maximum island elevation (Elev),

island isolation (D_NI), and island area (Area; Fig. 11). Overall, 14 of the 20 predictors were identified as important in this model, with 22 misclassified trees out of 500 (ROC=1).

Using the same dataset, modeling 500 classification trees, the best model for the island cluster group number derived from phylogenetic species dissimilarity distances response variable (UniFrac) was the all-available predictors model ('All (20)'; Table 1). This model indicated that the phylogenetic cluster group (UniFrac) response variable is most associated with the island area (Area), distance to Chukotka (D_Chu), maximum island elevation (Elev), the geologic age of the island (GeoA), and island isolation (D_NI; Fig. 11). Overall, 13 of the 20 predictors were identified as important in this model, with 13 misclassified trees out of 500 (ROC=1).

Discussion

Island systems have long inspired the study of ecology and evolution and probably have been studied disproportionately more than mainland areas (Darwin, 1859; Macarthur & Wilson, 1963; Simberloff, 1974; Warren et al., 2015; Weigelt et al., 2016). However, while in Alaska much attention has focused on the Aleutian Islands, many areas are still poorly known floristically. Three processes are ultimately responsible for the accumulation of species on islands: speciation, extinction, and dispersal (Ricklefs, 1987). The accumulated diversity within an island group can be measured as patterns of species richness (total number of species present in a community), species distributions, and variations in community assembly.

Species Richness – A total of 520 vascular plant species (231 genera and 69 families) are present on the 13 well-collected Aleutian Islands, which range across 51° and 55° N. Table 4 compares

the Aleutian Islands with other island groups, which indicates the large area, species poor character of the Aleutians. For the species richness response variable (Total_sp, regression), the best of the five models was the all non-categorical predictors model ('Non-categorical (15)'; Table 3). This model indicated that the species richness variable is most closely associated with island area (Area), distance to the Alaska Peninsula (D_AKP), island isolation (D_NI, distance to nearest island), and the total length of streams on the island (STR_KM; Fig. 11). The species-area curve for the Aleutians (Fig. 10) supports expectations under MacArthur and Wilson's equilibrium model of island biogeography (1967) that an island's distance from a mainland source of new immigrants, despite its size, is an important factor in species richness. We find an increase in logarithmic species number with log area and a linear trend was fit to the data, as has been observed with many other island studies (Fig.12; McNeill & Cody, 1978; Connor & McCoy, 1979; Rosenzweig, 1995).

To further analyze this expected relationship, the slope of the species-area curve would often be evaluated against the equilibrium model parameters (Connor & McCoy, 1979). Although this approach is useful for meta-analysis of multiple island groups (e.g. Matthews et al., 2016), its use as an analytical tool across a single island group is somewhat limited, since the logarithmic plot adjusts the dataset into a small area, which, while making complex data easy to view, does not greatly aid in fine-scale interpretation of the species-area relationship. In the current study, however, the TreeNet model outputs partial dependence plots that allow us to infer interactions between each individual predictor and the species richness more directly.

The partial dependence plot using the *island area* predictor indicated that, given the influence of the other predictors in the model, there is a plateau in species richness for island sizes ranging from ~300-1800 km^2 (Fig. 12). This is accompanied by a second plateau in species

richness at 2700 km^2 and greater in island size. In contrast to the logarithmic plot, the pattern of species richness and island area interactions is not linear, and we have identified two island size thresholds for further investigation. A three-phase species-area curve has been observed or evaluated in other ecological studies (Preston, 1960; Shmida & Wilson, 1985), although there has been some disagreement to the shape of phases and their causes (Storch, 2016). A 'flat-steep-flat' sigmoidal pattern has been described where species richness appears independent of island area for relatively small islands, and for collections from the largest islands (Lomolino, 2000b); as well as a 'steep-flat-steep' pattern, where island area and species richness are more dependent at either end of the curve (Fridley et al., 2005). The Aleutian Islands appear to have a 'steep-flat-steep' species-area curve in the partial dependence plot, where the species richness-island area interaction is adjusted for all other factors in the model (Fig. 12). The three size ranges of islands that fit the three slopes on the species area curve therefore may indicate appropriate starting points for finer scale analyses of species richness.

Island isolation, measured as the distance to the nearest island, was one of the most important variables in the best species richness model (Fig. 11). Island isolation is one of the equilibrium model variables (MacArthur and Wilson, 1967), and is often measured as distance to the mainland rather than between islands. Measured as inter-island distance, this isolation measure is not always strongly related to species richness – it had no effect on richness or similarity of islands on insular floras near Perth, Western Australia (Abbott, 1977).

As a different isolation measure, the distance from the Alaska Peninsula (D_AKP) was an important variable in the best species richness model (Fig. 11). The importance of the Alaska Peninsula distance variable indicates that it may be a primary "source" location for the Aleutians, and that geographic location along the east-west distribution of the chain is important for species

richness. This corresponds with a meta-analysis of over 17,000 of the world's marine islands, where richness was generally reduced on islands with increasing distance from the mainland (Weigelt et al., 2013). The Aleutian Islands share more species with the Alaska Peninsula than any other adjacent region. For islands such as Hainan Island, China, comparisons of the floristic similarity to adjacent potential source areas has been used as supporting evidence for the island's continental origin (Zhu, 2016).

As indicated by Stuessy et al. (1998), various geological, historical, and environmental factors may affect species richness and composition on islands in addition to the three variables put forth in the equilibrium model. In the best model for species richness in the Aleutians, the most important non-equilibrium model predictor was the island total stream length (Fig. 11). McCord (1980) proposed that the number of bays present on an island is a possible factor affecting the floristic composition in the Aleutian Islands. He noted that each bay or inlet has differing exposure characteristics associated with a particular floristic assemblage. Increasing bay number also results in a larger proportion of the island's mass having seashore riparian habitat. Similarly, he proposed that the stream lengths on each island may affect floristic composition, based on the observation that several rare species, particularly orchids such as *Cypripedium guttatum*, appeared only along streams (McCord, 1980). In the best species richness model, stream length (Str_km) was one of the most important predictors. In the cluster of correlated predictor variables (Fig. 5B), stream length (Str_km), was clustered with island area (Area). In the partial dependence plot for Str_km and species richness, however, it does not match the species-area curve pattern (Fig. 12). Instead there is a single plateau at approximately 200 km of stream length. Six of the thirteen islands examined had stream lengths exceeding that threshold. A meta-analysis of landscapes across the globe indicated that, in general, species

richness increases by 50% or more on average when riparian habitats are present by harboring different species pools than adjacent upland habitats (Sabo et al., 2005). It appears that the Aleutian Islands reflect this increase of species richness with increasing area of stream riparian habitat – though 200 km of stream length may represent the maximum limiting factor on species richness through streamside vegetation (Fig. 12). Additional floristic data collection in the Aleutian Islands should be guided by the testing of hypotheses that may be developed utilizing the results from this partial dependence plot and others using this dataset.

Species Distributions – Barriers to species distribution are often the focus of biogeography studies (e.g. van Welzen et al., 2005), and are often first identified by charting species distributions across a large area. It has been suggested that the Aleutian Islands have likely acted as a route for plant dispersal across the North Pacific in both directions (Heusser, 1990; Talbot et al., 2010a), where each mainland area likely acts as a "source" for the island assemblages, while the islands may act as "sinks" (Pulliam, 1988). The current dataset indicates a large number of species with either 'Eastern' or 'Western' distributions, and a large number of shared species between the entire study area and nearby regions, including the Alaska Peninsula (255 species) and the Aleutian-adjacent Russian Commander Islands (163 species; Fig. 9). On island groups such as the Kuriles, the island group species compositions also strongly reflects the character of mainland sources on either end, with influences from the Asian mainland and the Kamchatka Peninsula, which also represents the closest continental source to the western side of the Aleutian Islands. (Pietsch et al., 2003). In the Ryukyu Islands, which stretch between Taiwan and Japan's Kyushu Island, historical barriers within the island chain reflect strong differences in composition, and more closely resemble the closer mainland sources. In an analysis of the

Subantarctic islands, strong regional differences were observed based on the nearest continental sources (Van der Putten et al., 2010).

Using data from Hultén's *Flora of the Aleutian Islands* (1960), Lindroth (1961) recognized a unique pattern of plant distribution in the Aleutian Islands. North American endemic plant species were found in an increasing proportion of the flora with closer proximity to the Alaskan mainland, while Asian endemics increase in proportion towards Kamchatka (Lindroth, 1961). While the current dataset indicates that certain plant species are present in the western and eastern ends of the Aleutian chain that strongly reflect their adjacent mainland regions, such as the Kamchatka thistle (*Cirsium kamtschaticum*) and *Parasenecio auriculatus* reflecting an Asian character, the island species assemblages as a whole do not reflect an increasing number of shared species with the adjacent regions from east to west or west-east. There is, however, a trend of increasing proportion of shared species between islands and the Alaska Mainland from west to east across the island chain (See attached file Supplemental A).

In the Kuriles, which is also a largely volcanic island chain adjacent to Kamchatka, several major dividing lines have been proposed which separate the floristic character based on their continental sources; species diversity and character are similarly more reflective of the adjacent mainland sources, though this is emphasized by large climatic differences in the northern and southern ends of the island chain (Pietsch et al., 2003). Our model results suggest that east to west geographic location is generally associated with changes in Aleutian Island plant distribution. Modeling has indicated that the distance to the Alaska Peninsula predictor (D_AKP) is one of the most important variables using the species richness (Total_sp) response variable. Using the non-phylogenetic cluster group response variable (Jaccard), LGM_SL is the most

important variable in the best model, and appears to also indirectly approximate geographic location as the islands are generally grouped between the geographic gaps, east to west (Fig. 11).

It has been noted that several species are endemic to the Aleutians island chain, which often have extremely limited distributions (Talbot et al., 1995). In the current dataset, 37 species have a distribution limited to the two centrally located island groups (The Rat and Andreanof Islands; Fig. 1 & 8). These centrally located species may be there as a result of endemism, long distance dispersal, or reduced distributions following a historical extirpation from the surrounding island groups. One Aleutian endemic, *Polystichum aleuticum*, is listed as an endangered species, and has a single population on Adak Island (Talbot et al., 1995). The majority of island groups, which are highly isolated and have not been connected to a continent are the product of long distance dispersal events. This includes island groups such as the Hawaiian Islands, French Polynesia, and the Samoan Islands (Cowie & Holland, 2006). Isolated islands are also likely to support high numbers of endemic taxa, such as the Canary Islands, where 860 endemics comprise over half of the flora (Reyes-Betancort et al., 2008). In contrast, the Kuriles have 25 endemic species of vascular plants, which accounts for only 2% of the island group's 1367 species (Pietsch et al., 2003).

The term "two-way filter bridge," has been used for island chains where constraints limit the distributions of select plant species (such as the Hawaiian and Kurile Islands, Carlquist, 1965). It has been suggested that those species, which are well adapted to dispersing by wind and sea currents have readily dispersed across the Aleutian chain (Carlquist, 1965; Heusser, 1990; Talbot et al., 2010b). This is corroborated by the widespread distributions of several wind-dispersed species, such as *Salix arctica* and *Epilobium hornemannii* subsp. *behringianum*, both present on 12 of 13 islands in the study area. *Ligusticum scothicum* subsp. *hultenii*, one of the

three species present on all 13 islands in the study, is a diploid, seashore species that disperses by sea currents (Rydgren & Often, 1993), as predicted. In contrast, two other species present on all 13 islands, *Cardamine umbellata* and *Carex macrochaeta*, are unlikely to have been sea- or wind-dispersed, and may have been dispersed via the large migratory seabird and waterfowl populations (Carlsen et al., 2009). There are general dispersal patterns for highly isolated, oceanic island groups that reflect variables such as predominant wind patterns, island arrangements within groups, and bird migration routes (Cowie & Holland, 2006). The prevalence of seed dispersal types on these islands may also indicate the maximum general distance of each dispersal method. For instance, in Hawaii, the presence of few species which produce wind-dispersed seeds indicates a sharp decrease in transport over long distances, while large numbers of bird-transported fleshy seeds are present (Carlquist, 1967)

Species Composition – Species composition is an important floristic diversity measure that differs from species richness, as it measures the differences between species assemblages, even if species richness is the same. In a basic analysis of the species composition, the most frequently occurring genera and families in the Aleutian Islands study area are all three graminoid families (Poaceae, Cyperaceae, Juncaceae), three of the four graminoid genera (*Carex, Poa, and Luzula*), one shrub family and genus (Salicaceae, *Salix*), and several forbs and occasional shrub/subshrub families and genera, (Fig. 7). While graminoid species make up the most speciose families and genera, they are the second most common growth form in the Aleutian Islands; forbs account for 50.4% (Adak) to 65.9% (Kiska) of the species assemblage on each island. It is difficult to compare these proportions with other island groups, as island biogeography studies (e.g. Pietsch et al., 2003; Nakamura et al., 2009), and even floras of island groups rarely compile this

information using similar categories (e.g. Fosberg et al., 1975; Florence et al., 1995; Florence & Lorence, 1997; De Lange & Cameron, 1999). On the island of Hainan, China, which differs greatly in climate from the Aleutian Islands, the graminoid family Poaceae also has the most species in the flora, followed by Orchidaceae and Fabaceae (Zhu, 2016).

Species composition differences among the Aleutian Islands were approximated using several different methods. Using the UniFrac metric, which was phylogenetically determined, we expected that large differences in ecology between islands would be more evident. In both the UniFrac and Jaccard distance metric outputs, the highest dissimilarity was between the western island Alaid and the eastern island Unalaska. While being separated geographically, Unalaska is the second largest island in the study while Alaid is the smallest. Kiska and Agattu were the most similar in both the Jaccard and UniFrac outputs. Kiska and Agattu are located in the two westernmost island groups, and are similar in area (278 and 221.6 km^2). Given the comparisons above, even prior to modeling, it is apparent that geographic location and island area likely influence species composition (Fig. 4). This corresponds with other island groups stretched across large areas, where geographical lines may separate compositional groups (Pietsch et al., 2003; Nakamura et al., 2009; Webb & Ree, 2012).

There are several different lines of evidence that corroborate a palaeogeographic hypothesis for the observed diversification patterns in the Aleutian Islands: 1) periodic glaciation (and associated drops in sea level; Hultén, 1937; Lindroth, 1961), 2) volcanic eruptions (Hultén, 1937; Heusser, 1990), and 3) climate change (Heusser, 1990). Using the current dataset, modeling for patterns of community similarity with non-phylogenetic cluster groups (Jaccard) indicated that the landmass groups during the last glacial maximum (LGM_SL), which formed during periods of lowered sea level, were the most important predictors. Geologic age (GeoA)

was one of the most important predictors for the phylogenetic cluster group (UniFrac) response variable's best model. These results pertaining to landmass group during the LGM echo findings by Weigelt et al. (2016), who examined estimated LGM coastlines of 184 studied islands worldwide, which experienced strong post-LGM changes in most physical and bioclimatic conditions as a result of sea level rise. They found an expected increase in species richness with increasing historical area due to increased LGM area as compared with the present area. The most species rich island in the Aleutians, Unalaska, was connected to the Alaskan mainland historically (Fig. 1), and species richness was associated with distance from the Alaska Peninsula in the TreeNet modeling, which may fit this expected relationship.

Conclusion

Aleutian plant species distribution patterns may be best explained by their patterns of presence across the four major island groups (Fig. 1). The most common distribution being the 'Eastern', though it compared similarly to the 'Western' (Fig. 8). Other island groups have similar distributional patterns between continental source areas (e.g. Pietsch et al., 2003; Nakamura et al., 2009). The four major island groups are also important to species composition, as species composition is more similar between geographically closer islands in the Aleutians, particularly for those island groups that were linked by land during the last glacial maximum. The last glacial maximum landmass predictor along with maximum island elevation, island isolation, and island area were found to be most important for species composition. Similarly, phylogenetic-based species composition was associated with islands that were of the same geological age. The older islands in the chain are mostly constrained to the western Aleutian island groups.

While Aleutian plant species richness is strongly associated with the equilibrium model variables area and island isolation, as well as distance from the islands to the Alaska Peninsula, modeling also indicated that island total stream length was one of the most important predictors, suggesting that the diversity of ecological niches may play an important part in determining total richness. The plateaus and patterns within the area and island total stream length partial dependence plots for this measure provide targets for further investigation.

Although this study included a compilation of over eighty years of collecting efforts, it highlights how few "complete" floras have been conducted in the Aleutian Islands- although many single event collections have been made, most have been restricted along the shorelines due to time and transportation limitations. To expand upon this study, additional collecting should be conducted completely across islands which may provide further insight into the conclusions here; monitoring studies should also be conducted for the uncommon and endemic species to reveal historical relationships and to clarify conservation concerns. As introduced predators and cattle have been eliminated from islands, or are being introduced (e.g. Ricca et al., 2012) baseline-sampling efforts should also be conducted towards monitoring for recovery and impacts.

This study, as an application of modern modeling techniques and data collection and digitization, has highlighted the primary factors that drive floristic distribution, composition, and diversity, across the Aleutians. The remote Aleutian Islands chain will continue to be difficult to access and subject to inclement weather. Yet, conclusions presented here highlight exciting future research targets for gaining continued insights into diversity patterns across the Aleutians.

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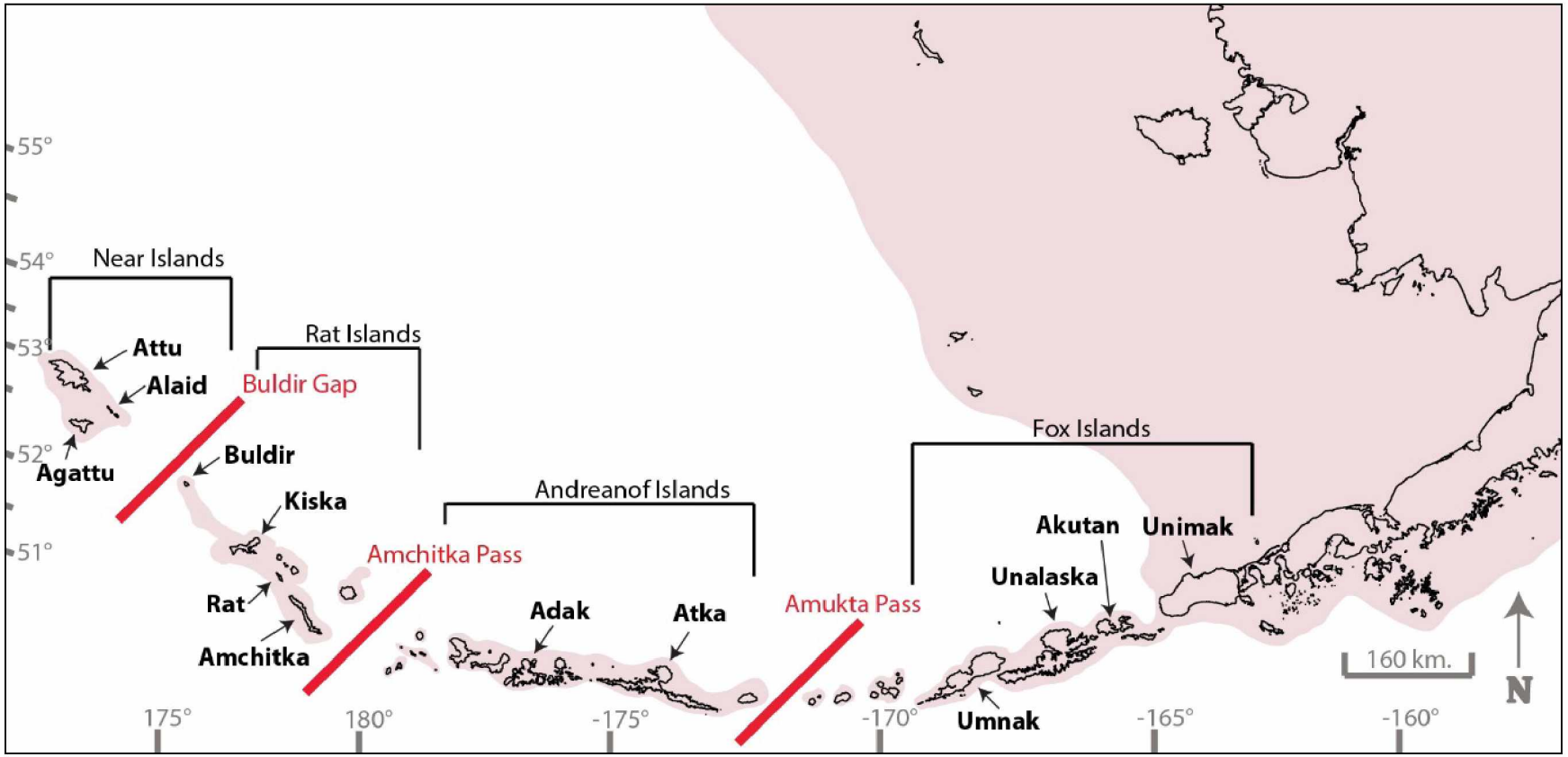

Figure 1 Map of the Aleutian Islands. This map identifies the 13 Islands, which were determined to be "well-collected", as indicated by the abundance of documented voucher specimens. Island groups that include at least one island in the study are labeled. The three geographic gaps between island groups are also identified. The pink shading indicates areas, which were expected to be above sea level during the last glacial maximum's estimated lower sea level depths (~10-25,000 years ago).

Figure 2 Modes of transportation to and "accommodation" on the Aleutian Islands. Fieldwork was conducted in the Aleutian Islands in the summers of 2010-2011. Travel from Adak west to Attu was provided by the U.S. Fish and Wildlife Service (USFWS) Alaska Maritime National Wildlife Refuge Vessel Tiglax (A), photo taken from Attu. Travel to the islets near Buldir Island and around the coast of the island were conducted by inflatable rafts launched from shore (B). (C) Buldir Island USFWS camp and the author's camp and supplies, 2010-2011.

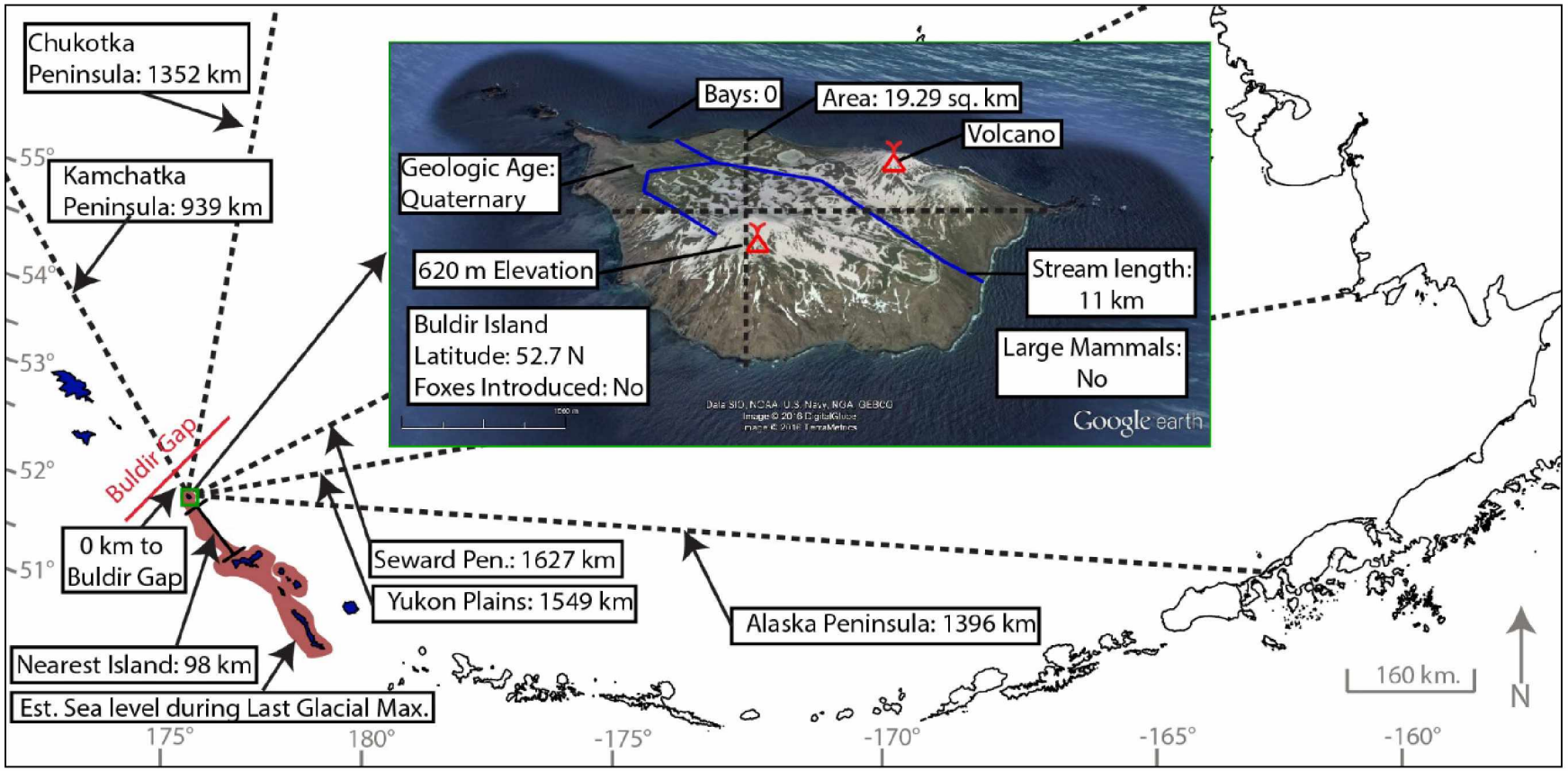

Figure 3 Buldir Island predictor variables used. Potentially explanatory variables associated with Buldir Island are indicated on the map of the Aleutians and island specific explanatory variables are shown in the insert map of Buldir. Variables were identified as predictors by island biogeography studies in other regions and historical Aleutian Island studies. These variables were collected for each of the islands in the study.

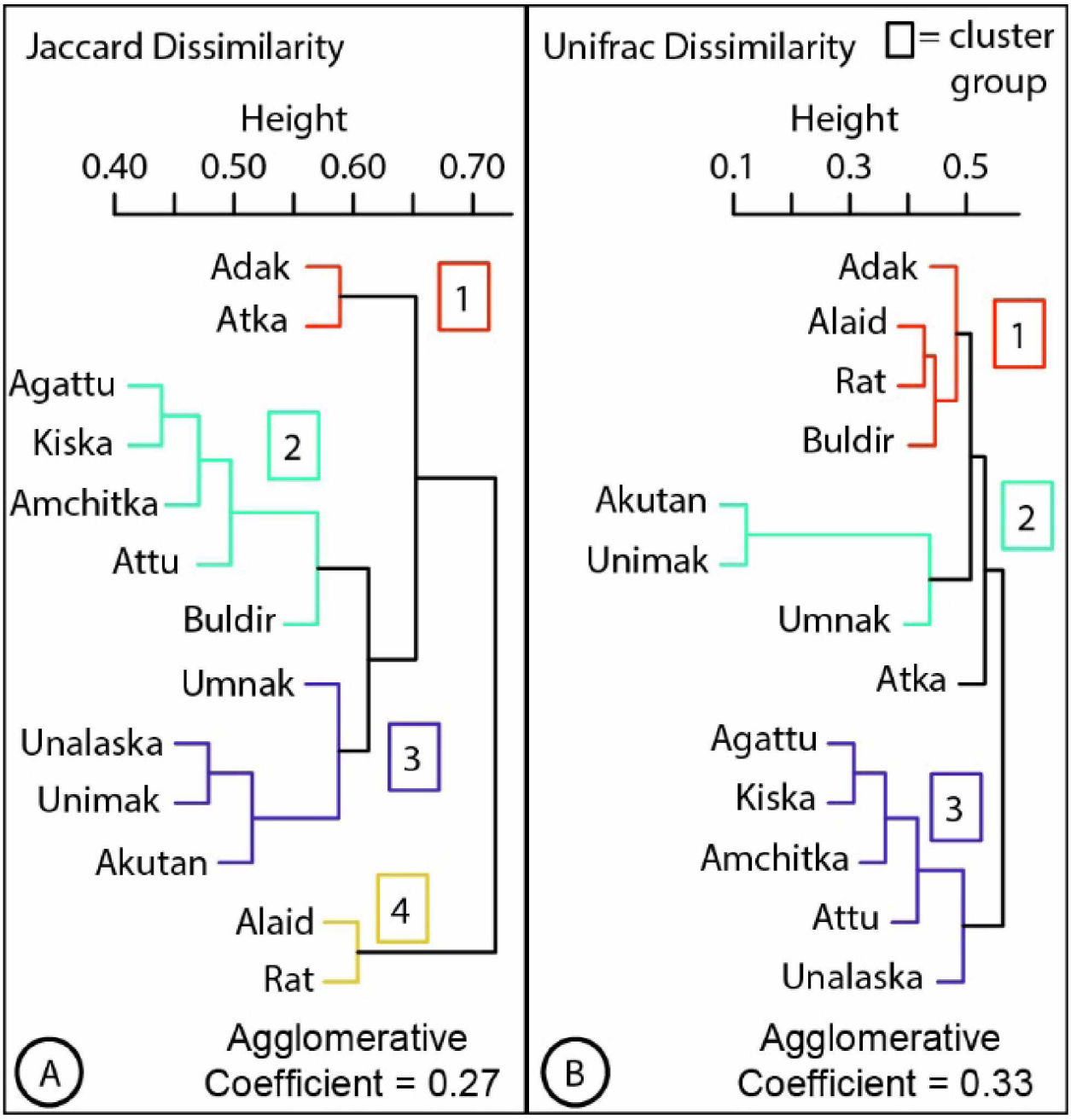

Figure 4 Aleutian Islands plant species dissimilarity clusters. These cluster dendrograms were calculated from dissimilarity matrices using Unweighted Pair Group Mean Averaging (UPGMA). Tree (A) was calculated from a Jaccard dissimilarity matrix, using the vascular plant species presence/absence on each island. Tree (B) was calculated from an unweighted UniFrac distance matrix, as an approximation of the phylogenetic diversity of the plant species between islands. Numbers within colored boxes were used as input response variables for the analyses as the the island cluster group number, i.e, non-phylogenetic (A) and phylogenetic (B) cluster groups. The agglomerative coefficient is a unitless measurement of the strength of the dendrogram, produced by the clustering function.

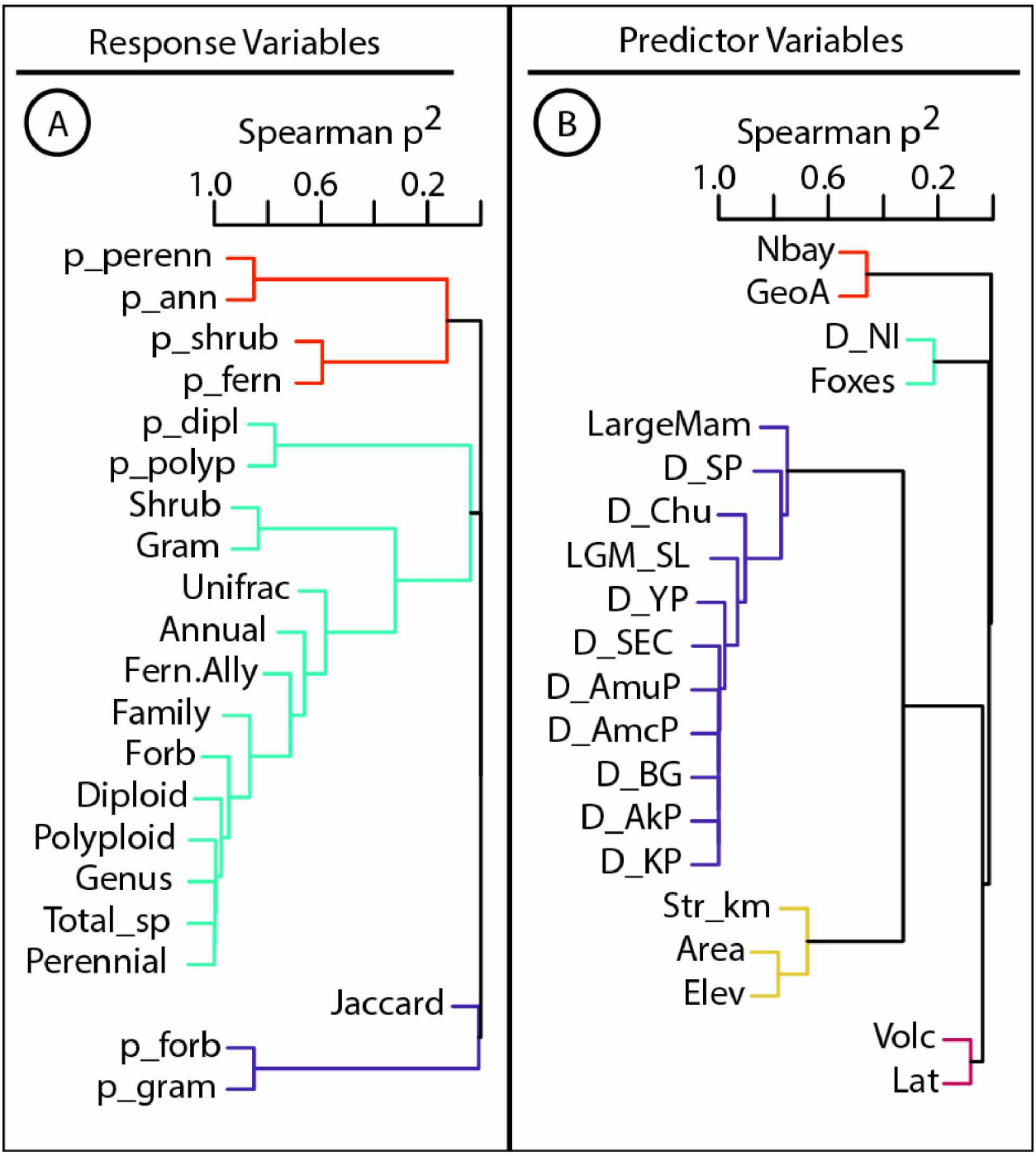

Figure 5 Output of the varclus function showing correlated response variables (A) and predictors (B). (A) Dependent, response variables that may be used as target variables in modeling. (B) Independent, predictors. The Spearman P^2 scale indicates the strength of correlation at the branches within each cluster.

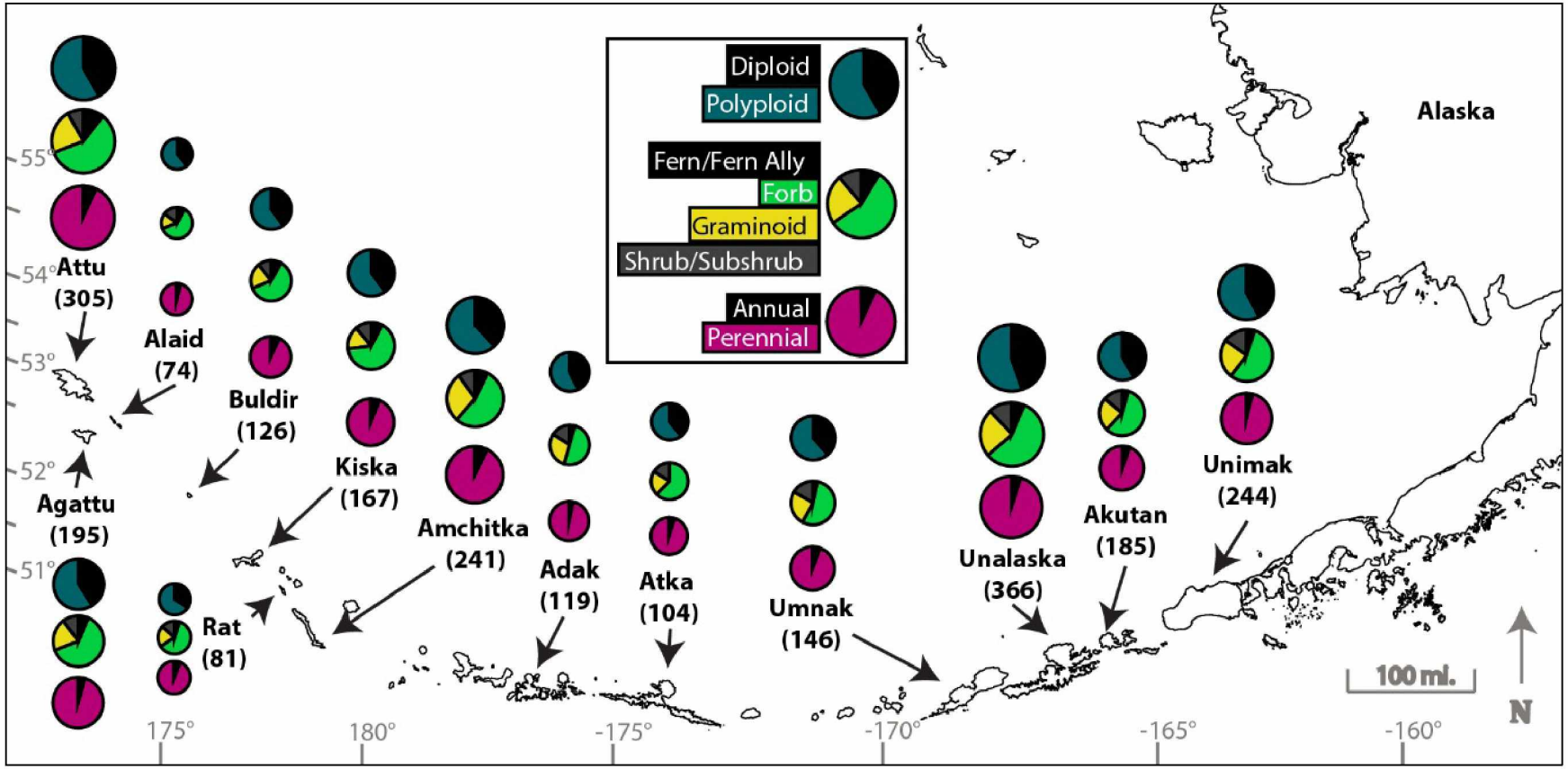

Figure 6 Aleutian Islands plant growth and ploidy proportions by island. Total species richness is given in parentheses and is proportional to the diameter of the pie chart.

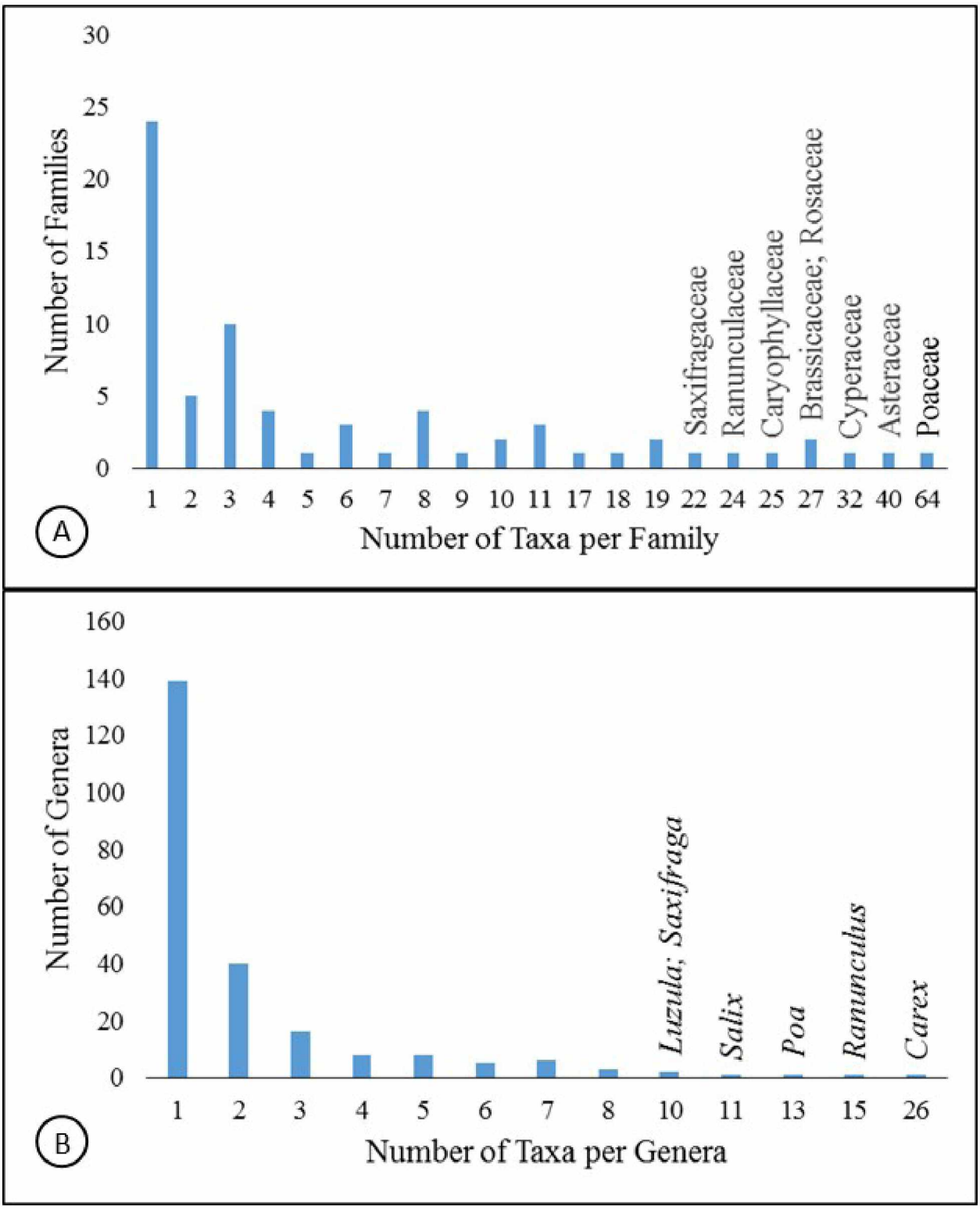

Figure 7 Number of plant species in the Aleutian Islands per genus (A) and family (B). (A) The families with the highest number of taxa (22-64) are labeled. (B) Items 10-26 are selected for genera with the highest number of taxa within.

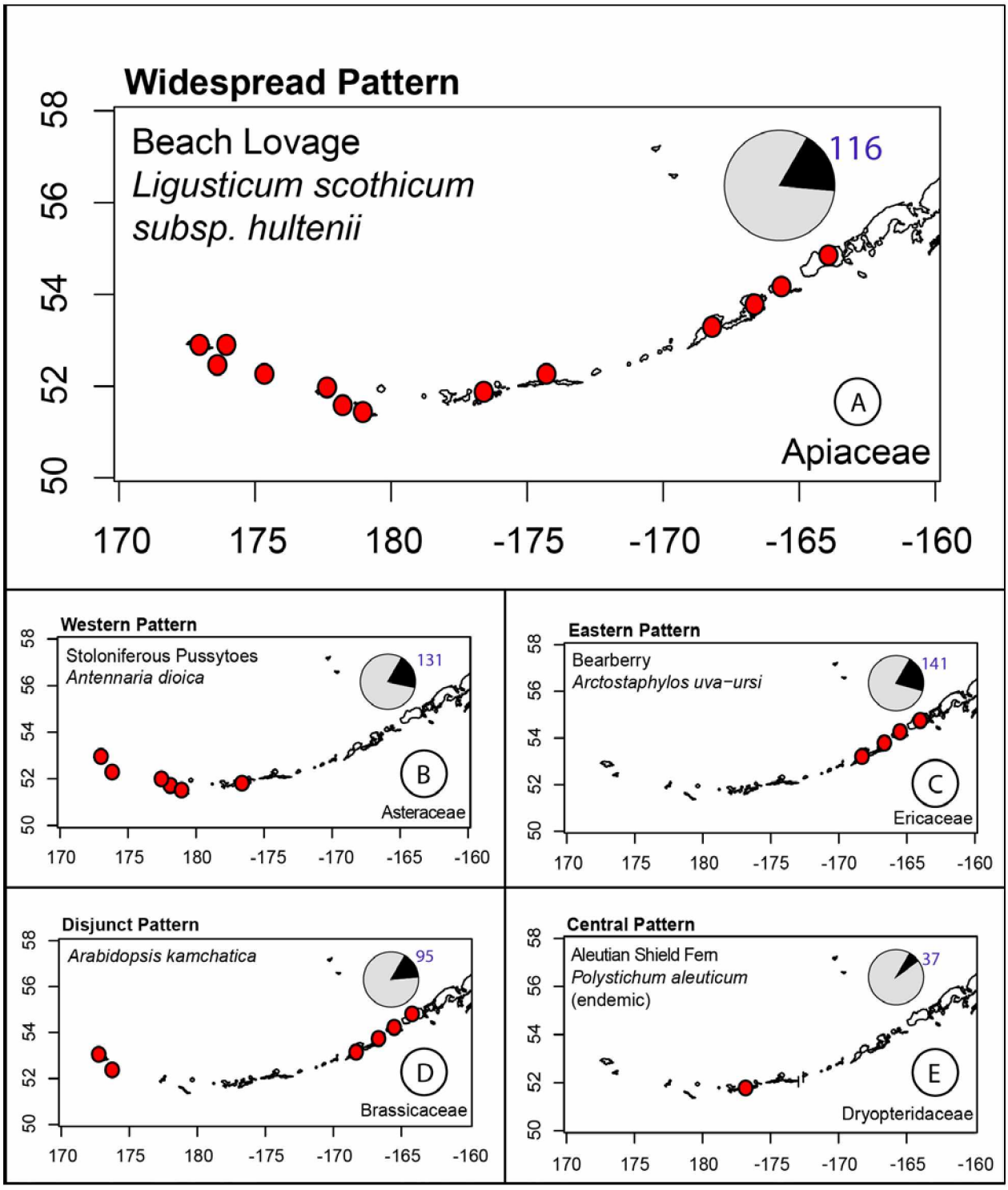

Figure 8 Plant species distribution patterns within the Aleutian Islands represented by exemplar taxa. (A) Widespread, (B) Western, (C) Eastern, (D) Disjunct, (E) Central. Several of the centrally distributed species are Aleutian endemics. See attached Supplemental File A for a complete set of species distributions.

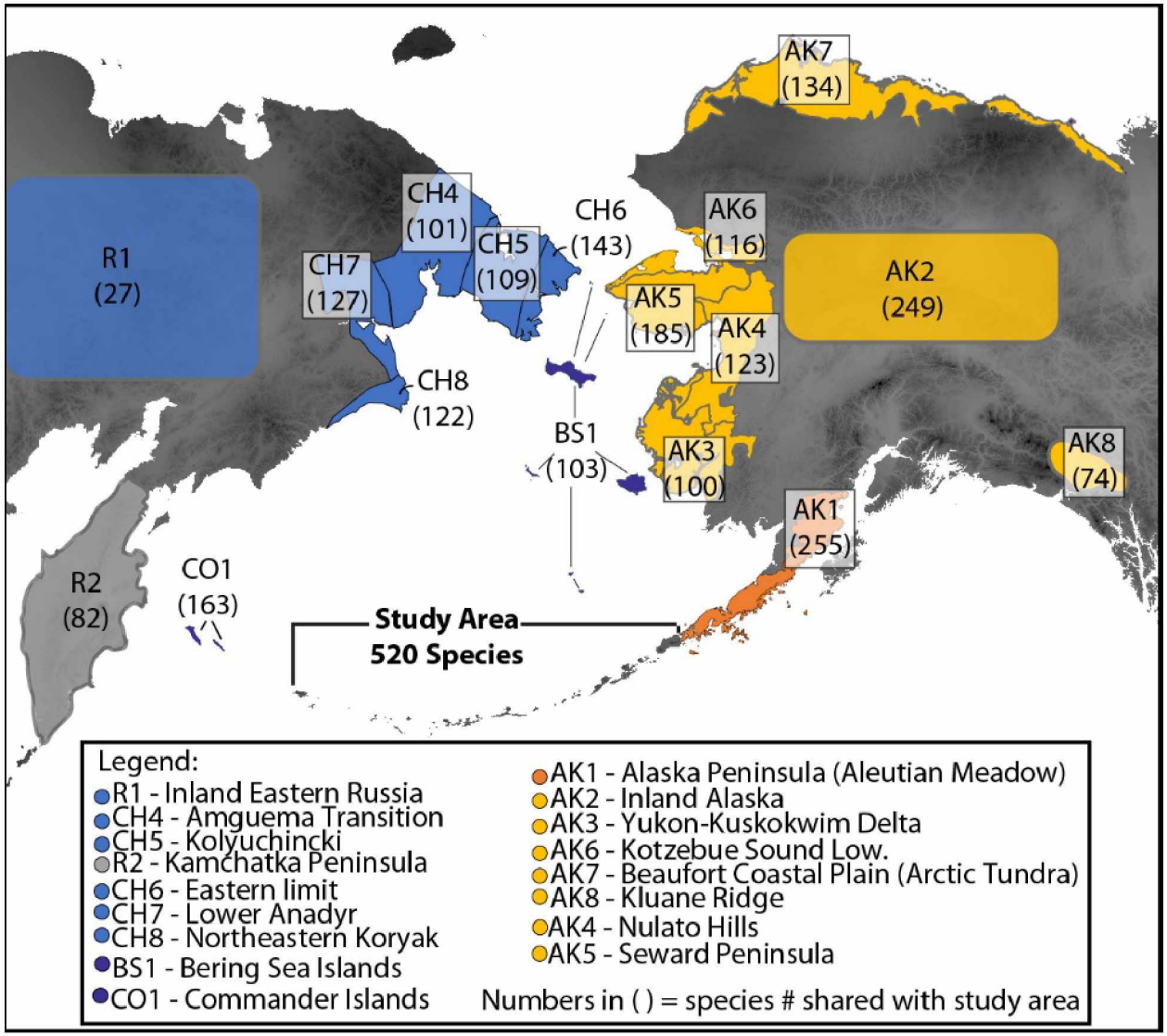

Figure 9 Plant species shared between the Aleutian Islands and adjacent regions. Numbers in parentheses reflect the total number of shared species between the study area and the region. Adapted from Ickert-Bond et al. (2013).

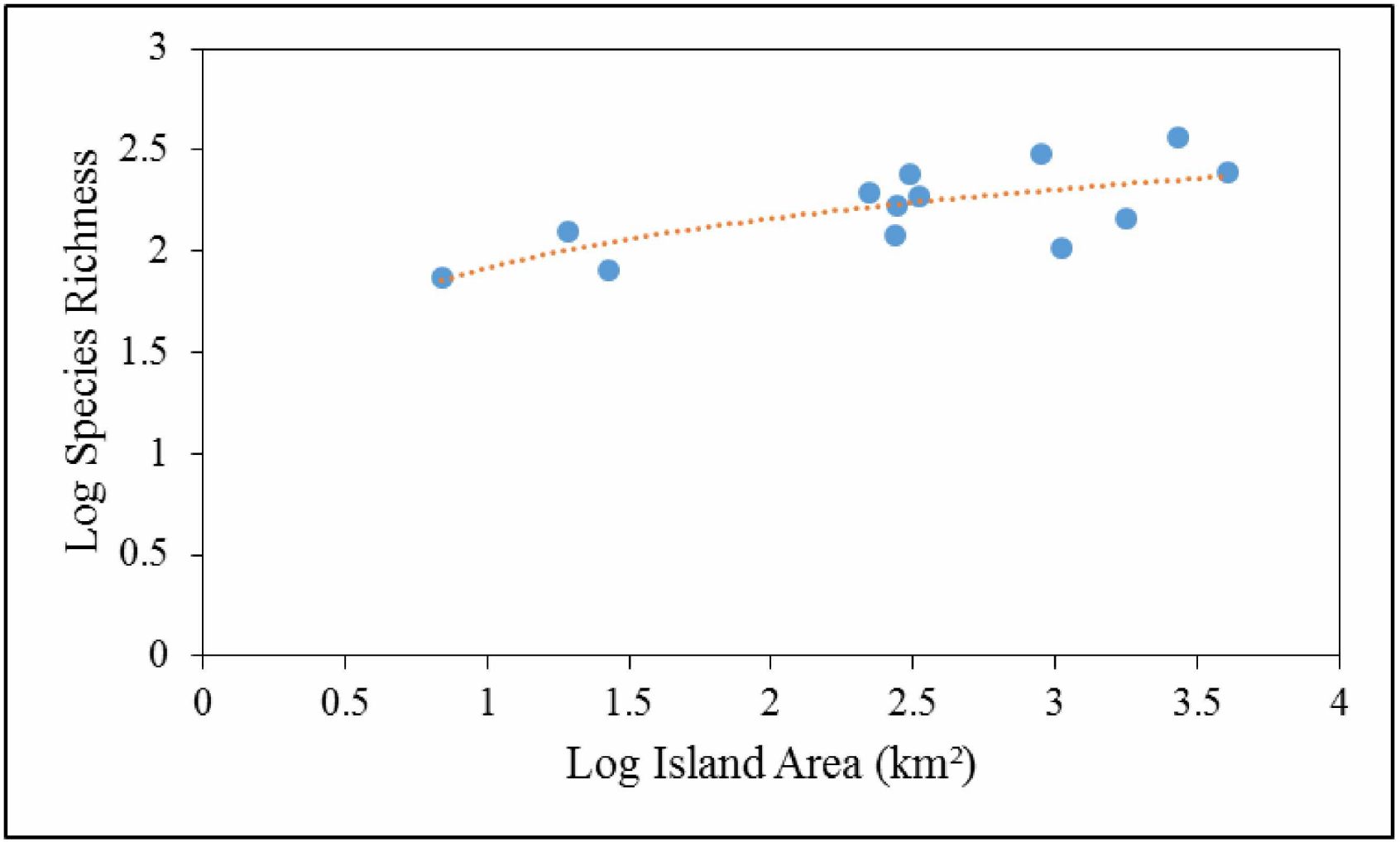

Figure 10 Aleutian Islands plant species log area/log species richness plot. A logarithmic trend line was added (R^2=0.51).

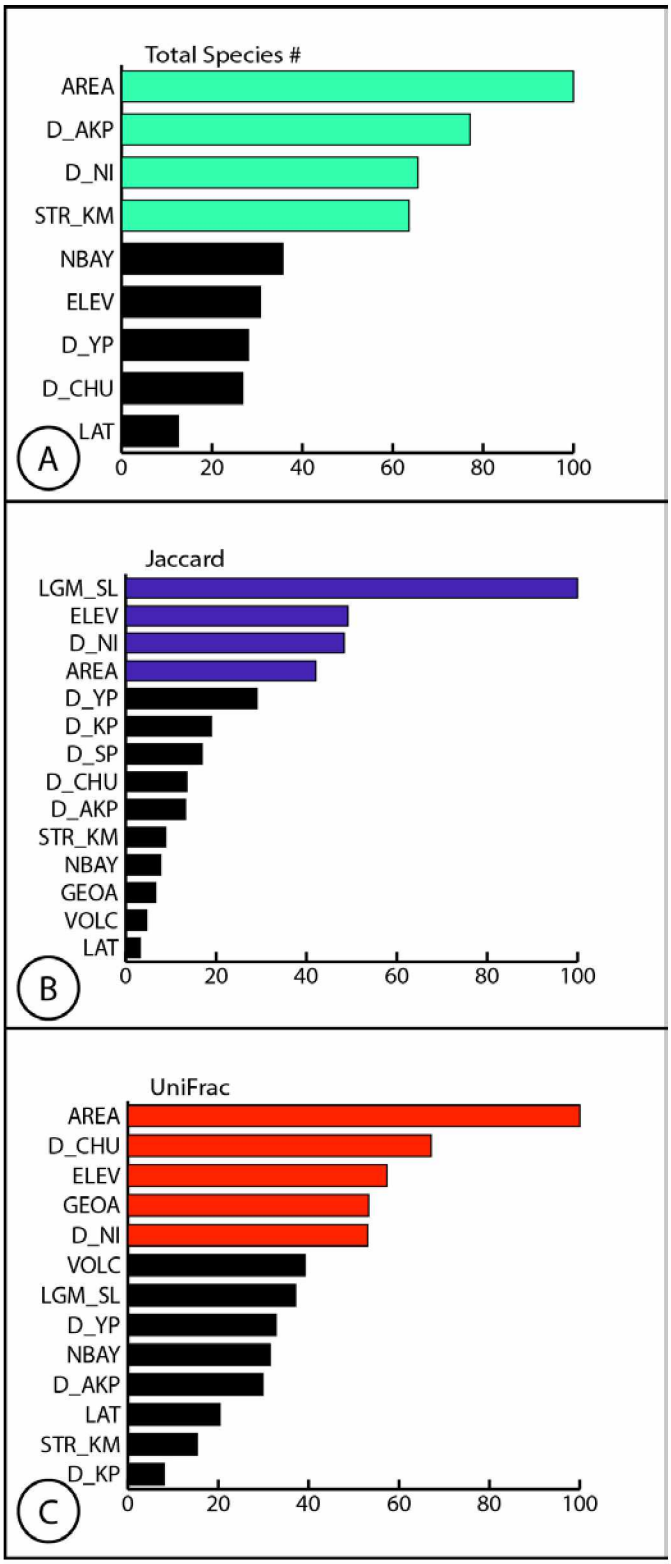

Figure 11 Aleutian plant species variable importance plots for three response variables. Predictors with highest importance are presented in color. Total species number (A), Jaccard-based non-phylogenetic cluster group (B), and UniFrac-based phylogenetic cluster group (C). The x-axis denotes importance (unitless).

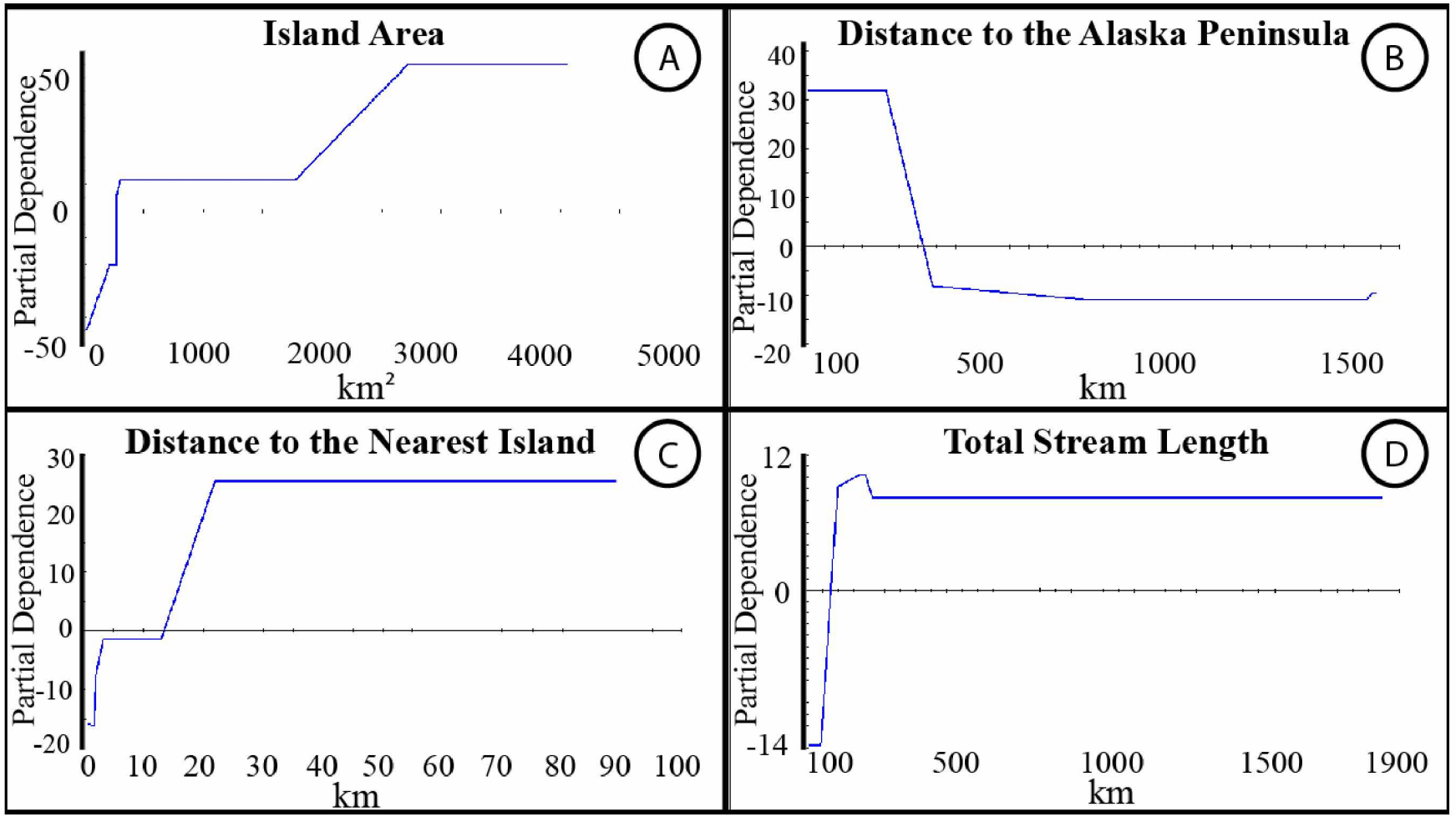

Figure 12 Partial dependence plots for Aleutian plant species richness. Plots for the four most important variables are visualized here. The 'Partial Dependence' axis (y axis) indicates the relatedness of species richness on a logit scale with the predictor, adjusted by the averaged effects of all other predictors in the model (unitless). Island area (A); Distance to the Alaska Peninsula (B); Distance to the Nearest Island (C); Total Stream Length (D).

Table 1 Predictors included in the various TreeNet models. Abbreviations: Island=island name; Area=island area (km2); LGM_SL= Island/landmass connected during the lowest sea water level during the last glacial maximum; Elev=maximum island elevation (m); Volc=volcanic islands (0/1); D_AkP=distance from the Alaska Peninsula (km); D_KP=distance from the Kamchatka Peninsula (km); D_YP=distance to the Yukon Plain (km); D_SP=distance from Alaska's Seward Peninsula (km); D_Chu=distance to the Chukotka Peninsula (km); D_NI=distance to the nearest island (km); D_BG=distance from the Buldir Gap (km); D_AmcP=distance from Amchitka Pass (km); D_AmuP=distance from Amukta pass (km); Nbay=number of bays on the island; Str_km=mapped stream length (km); GeoA=geologic age of the island; Lat=island latitude; Foxes= Islands which have had foxes introduced or native fox populations (0/1); LargeMam= large hooved mammals have been introduced or are native to the island (0/1).

Island	Area	LGM_SL	Elev	Volc	D_AkP	D_KP	D_YP	D_SP	D_Chu	D_NI
Adak	274.59	3	1196	2	935	1422	1261	1468	1506	1.3
Agattu	221.60	1	632	0	1528	789	1642	1687	1327	27
Alaid	6.90	1	29.6	0	1511	796	1616	1658	1299	1
Amchitka	309.00	2	300	0	1213	1140	1475	1624	1499	22
Atka	1048.80	3	1533	1	758	1512	1137	1385	1535	1.8
Attu	893.00	1	860	0	1538	702	1633	1666	1289	30
Buldir	19.29	2	620	2	1396	939	1549	1627	1352	98
Kiska	278.00	2	1220	1	1314	1054	1491	1586	1393	1
Rat	26.70	2	206	0	1260	1118	1429	1682	1473	13
Umnak	1776.76	4	2149	1	340	1889	881	1231	1639	4.5
Unalaska	2720.00	4	1800.1	1	215	1947	805	1167	1618	3.3
Akutan	334.13	4	1303	1	174	2037	773	1154	1655	2.1
Unimak	4069.90	4	2856.9	1	3	2101	676	1075	1633	0.6
Mean:	**921.44**	**-**	**1131.20**	**-**	**937.31**	**1342.00**	**1259.08**	**1462.31**	**1478.31**	**15.82**
St.Dev.:	**1237.92**	**-**	**816.95**	**-**	**572.82**	**509.04**	**361.42**	**230.74**	**135.10**	**26.89**
max:	**4069.90**	**-**	**2856.90**	**-**	**1538.00**	**2101.00**	**1642.00**	**1687.00**	**1655.00**	**98.00**
Min:	**6.90**	**-**	**29.60**	**-**	**3.00**	**702.00**	**676.00**	**1075.00**	**1289.00**	**0.60**

Table 1 Continued (2 of 2)

Island	D_BG	D_AmcP	D_AmuP	Nbay	Str_km	GeoA	Lat	Foxes	LargeMam
Adak	490	247	-358	15	211	3	51.8	1	1
Agattu	-143	-410	-1010	2	100	2	52.5	1	0
Alaid	-133	-409	-998	0	4	1	52.7	1	0
Amchitka	198	0	-646	5	187	2	51.3	1	0
Atka	595	367	-184	21	321	2	52.3	1	1
Attu	-173	-443	-1032	10	170	2	52.5	1	0
Buldir	0	-265	-864	0	11	1	52.7	0	0
Kiska	98	-143	-759	5	100	2	52.2	1	0
Rat	163	-88	-709	3	10.5	2	51.5	1	0
Umnak	1012	801	154	10	1845	3	53.3	1	1
Unalaska	1100	889	251	50	403	2	53.8	1	1
Akutan	1210	915	391	3	46	1	54.2	1	1
Unimak	1300	1107	481	4	551	2	54.8	1	1
Mean:	**439.77**	**197.54**	**-406.38**	**9.85**	**304.58**	**-**	**52.74**	**-**	**-**
St.Dev.:	**548.61**	**563.70**	**563.45**	**13.52**	**491.41**	**-**	**1.04**	**-**	**-**
max:	**1300.00**	**1107.00**	**481.00**	**50.00**	**1845.00**	**-**	**54.80**	**-**	**-**
Min:	**-173.00**	**-443.00**	**-1032.00**	**0.00**	**4.00**	**-**	**51.30**	**-**	**-**

Table 2 Species richness, species composition cluster groups, and other categorical response variables. Island=island name; Total_sp=total number of species; Jaccard=Jaccard dissimilarity based non-phylogenetic cluster group; UniFrac=UniFrac distance-based phylogenetic cluster group; Family=number of families; Genus= genera; Perennial=perennial taxa; Annual=annual taxa; p_perenn=proportion of perennials to annuals; p_ann=proportion of annuals to perennials; Forb=forb taxa; Shrub=shrub and subshrub taxa; Gram=graminoid taxa; Fern.Ally=fern and fern ally taxa; p_forb=proportion of forbs vs. shrubs and subshrubs, graminoid, and fern/fern ally taxa; p_shrub=proportion of shrub taxa; p_gram=proportion of graminoids; p_fern=proportion of fern and fern ally taxa; Diploid=diploid taxa; Polyploid=polyploid taxa; p_dipl=proportion of diploid to polyploid taxa; p_polyp=proportion of polyploid taxa. Mean=the average value for the variable; St.Dev.=the standard deviation of the range of values; max=maximum value per variable; Min=minimum value per variable.

Island	Total_sp	Jaccard	UniFrac	Family	Genus	Perennial	Annual	p_perenn	p_ann	Forb	Shrub
Adak	119	1	1	38	83	116	4	0.97	0.03	60	19
Agattu	195	2	3	45	119	189	9	0.95	0.05	123	20
Alaid	74	4	1	31	63	74	3	0.96	0.04	45	11
Amchitka	241	2	3	52	128	230	18	0.93	0.07	131	24
Atka	104	1	2	29	73	100	5	0.95	0.05	65	17
Attu	305	2	3	53	155	290	22	0.93	0.07	179	24
Buldir	126	2	1	33	83	121	9	0.93	0.07	77	13
Kiska	167	2	3	45	113	160	10	0.94	0.06	110	19
Rat	81	4	1	30	65	78	5	0.94	0.06	50	11
Umnak	146	3	2	36	102	139	9	0.94	0.06	80	24
Unalaska	366	3	3	60	189	350	19	0.96	0.05	210	43
Akutan	185	3	2	41	117	178	10	0.96	0.05	107	26
Unimak	244	3	2	52	142	238	9	0.98	0.04	136	37
Mean:	**181.00**	**-**	**-**	**41.92**	**110.15**	**174.08**	**10.15**	**0.95**	**0.05**	**105.62**	**22.15**
St.Dev.:	**88.06**	**-**	**-**	**10.13**	**37.50**	**83.76**	**5.97**	**0.02**	**0.01**	**50.12**	**9.41**
max:	**366.00**	**-**	**-**	**60.00**	**189.00**	**350.00**	**22.00**	**0.98**	**0.07**	**210.00**	**43.00**
Min:	**74.00**	**-**	**-**	**29.00**	**63.00**	**74.00**	**3.00**	**0.93**	**0.03**	**45.00**	**11.00**

Table 2 Continued (2 of 2)

Island	Gram	Fern.Ally	p_forb	p_shrub	p_gram	p_fern	Diploid	Polyploid	p_dipl	p_polyp
Adak	35	5	0.50	0.16	0.29	0.04	49	65	0.43	0.57
Agattu	40	13	0.63	0.10	0.20	0.07	78	113	0.41	0.59
Alaid	12	6	0.61	0.15	0.16	0.08	28	43	0.39	0.61
Amchitka	69	18	0.54	0.10	0.29	0.07	91	147	0.38	0.62
Atka	22	0	0.63	0.16	0.21	0.00	40	61	0.40	0.60
Attu	70	33	0.58	0.08	0.23	0.11	126	176	0.42	0.58
Buldir	26	10	0.61	0.10	0.21	0.08	50	74	0.40	0.60
Kiska	26	13	0.65	0.11	0.15	0.08	65	97	0.40	0.60
Rat	17	4	0.61	0.13	0.21	0.05	25	48	0.34	0.66
Umnak	37	5	0.55	0.16	0.25	0.03	56	90	0.38	0.62
Unalaska	90	24	0.57	0.12	0.25	0.07	168	207	0.46	0.57
Akutan	44	8	0.58	0.14	0.24	0.04	79	109	0.43	0.59
Unimak	59	12	0.56	0.15	0.24	0.05	109	147	0.45	0.60
Mean:	**42.08**	**11.62**	**0.59**	**0.13**	**0.23**	**0.06**	**74.15**	**105.92**	**0.41**	**0.60**
St.Dev.:	**23.50**	**9.05**	**0.04**	**0.03**	**0.04**	**0.03**	**41.20**	**50.76**	**0.03**	**0.02**
max:	**90.00**	**33.00**	**0.65**	**0.16**	**0.29**	**0.11**	**168.00**	**207.00**	**0.46**	**0.66**
Min:	**12.00**	**0.00**	**0.50**	**0.08**	**0.15**	**0.00**	**25.00**	**43.00**	**0.34**	**0.57**

Table 3 Score summaries for five Aleutian plant assemblage TreeNet models. Total_sp=species richness; Jaccard=non-phylogenetic cluster group based on Jaccard dissimilarity species composition; UniFrac=phylogenetic cluster group based on UniFrac distance species composition; ROC=receiver operating characteristic; MSE=mean squared error; Avg. LL (Neg.)=average negative log likelihood. Red asterisks indicate the best model.

Model	Response Variable	Important Predictors	ROC	MSE	R^2	Best Model
All (20)	Total_sp	13	0.87	2613.25	0.57	
Non-categorical (15)	Total_sp	9	0.93	2297.55	0.62	*
Equilibrium (3)	Total_sp	3	0.78	2334.63	0.62	
Ecological Niche (6)	Total_sp	6	0.97	3589.07	0.41	
Disruption (4)	Total_sp	3	0.08	6158.57	-0.01	
Model	**Response Variable**	**Important Predictors**	**ROC**	**Misclassified Trees**	**Avg LL (Neg.)**	**Best Model**
All (20)	Jaccard	14	1	22	0.01	*
Non-categorical (15)	Jaccard	11	1	24	0.01	
Equilibrium (3)	Jaccard	3	1	247	0.09	
Ecological Niche (6)	Jaccard	6	1	70	0.04	
Disruption (4)	Jaccard	4	1	102	0.64	
All (20)	UniFrac	13	1	13	0.07	*
Non-categorical (15)	UniFrac	11	1	17	0.09	
Equilibrium (3)	UniFrac	3	1	47	0.11	
Ecological Niche (6)	UniFrac	6	1	99	0.10	
Disruption (4)	UniFrac	3	0.86	33	0.43	

Table 4 Summary statistics for the Aleutian Islands compared to other island groups. *The Aleutian Islands totals for Area and Islands are based on the current study area and would be much larger if all Aleutian Islands were included.

Island Group	Reference	Species	Genera	Families	Length	Islands	Area	Species per km^2
Aleutian Islands [USA]*	-	520	231	69	1600	13	11979	0.04
Ryukyu Islands [Japan]	Nakamura et al., 2009	1815	790	167	1300	26	4434	0.41
Kuriles [Russia]	Pietsch et al., 2003	1367	550	135	1200	56	15600	0.09
Galapagos Islands [Ecuador]	van der Werff, 1983	591	N/A	N/A	300	18	7846	0.08
Juan Fernandez Islands [Chile]	Stuessy et al., 2008	383	234	73	200	3	99.6	3.85
Marquesa Islands [French Polynesia]	Florence & Lorence, 1997	351	177	85	380	12	1300	0.27

General Conclusion

In this study we aimed to increase botanical knowledge of the Aleutians and determine significant historical and current geographical factors associated with species diversity and richness in the Aleutian Islands. Results from our collection efforts were consolidated with previous species lists (published and unpublished), and a review of museum collections to generate a comprehensive species list for the Aleutian Islands totaling 520 records for thirteen islands. For the thirteen islands in the study, this compilation is an expansion of previous attempts at complete compilations of Aleutian species (Hultén, 1960; McCord, 1980), and represents the most current flora. Calculating the flora as measures of species richness and species composition between islands, we modeled the significant historical and current geographical factors most associated with species diversity and richness in the Aleutian Islands to be the equilibrium model-associated predictors island area, distance to the nearest island, and distance to the mainland. Species richness was also associated with a habitat variable – the total length of streams per island, which has been confirmed as a diversity-increasing trait in landscapes globally (Sabo et al., 2005). Both measures of species composition also were associated with maximum island elevation, which may also be a measure of habitat diversification. The phylogenetic species composition measure was also associated with the equilibrium model variable of island age, while the classic species composition measure was also closely associated with the landmass groups during the last glacial maximum. Species richness and composition in the Aleutians, as expected, could be approximated with the classic island biogeography equilibrium model; but we were also able to approximate the most important factors that are not part of the equilibrium model and were determined from an evaluation of the Aleutian's local geology, regional geology, and human history.

Working on the Aleutian floristic project has resulted in the completion of several other projects beneficial to the Alaska scientific community. This included the publication of a paper which assembled and compared the floras of the Western Aleutian Islands and the Bering Sea Islands, following two summers of field work in the Aleutian Islands and a trip to St. Paul, St. Matthew, and Hall Islands in the Bering Sea by the author (Garroutte & Ickert-Bond, 2013). The field efforts by the author also resulted in collections of approximately 250 specimens for preservation at the University of Alaska Museum of the North (ALA), and also resulted in the collection of DNA material for multiple plant lineages currently under study in the Ickert-Bond lab, including material for a current graduate study on the genus *Therorhodion*.

The flora of the Aleutian Islands has also been bolstered on several islands by collection efforts of the author and many other researchers who coordinated their efforts with the authors and ALA. The digitization and taxonomic standardization of multiple printed texts on the Aleutian flora (See attached file Supplemental A) should also make future analyses of the Aleutians much easier. Despite these efforts, there is still little information on the flora of Semisopochnoi Island (the largest of the active volcanoes in the central and western Aleutian arc; Delong et al., 1985), as well as Tanaga, Kanaga, or Great Sitkin Island. Travel and field work in the harsh climate of the Aleutian and Bering Sea Islands remains expensive and constrained by short seasons.

There are several exciting avenues of proposed work that could lead from the current effort. As noted above, the compilation of validated digitized data (Supplemental A) allows for easy comparisons and meta-analyses, and provides a base for additions. Furthermore, species richness may be calculated for other abundant species groups on the Aleutian Islands. Our conclusions regarding predictor importance for Aleutian vascular plant species may then be

tested as predictions for other species groups. Approximations of the non-phylogenetic (Jaccard) and phylogenetic (UniFrac) cluster group measurements of species diversity may also be calculated, though sensitivity testing should be conducted to ensure repeatability. The dataset and analyses from this effort also highlight a number of interesting patterns that would be very interesting to examine further with phylogeographic approaches using molecular sequencing. For example the Aleutian endemic *Saxifraga aleutica*, which appears as sister to the Siberian *Saxifraga serphyllifolia* subsp. *glutinosa*, shows a Western distributional pattern within the Aleutian chain. When looking at a recent phylogeny (Tkach et al., 2015) this species appears as sister to the Siberian *Saxifraga serphyllifolia* subsp. *glutinosa*, but the position is unresolved in regards to the *Saxifraga serphyllifolia* subsp. *serpyllifolia* that has an amphiberigian distribution. Using a phylogeographic approach, one would be able to test the colonization over time from either Western or Eastern Beringia. As more data becomes digitized and accessible, through efforts like this thesis, improved meta-analyses and biogeographic studies may be designed to more fully understand historical processes that led to current patterns of floristic diversity and community assemblage in Alaska.

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